

The American Midland Naturalist

Devoted to Natural History

Primarily that of the Prairie States

Founded by J. A. Nieuwland, C.S.C.

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JANUARY, 1941

NO. 1

The Genus *Carex* in Michigan

Frederick J. Hermann

Since the publication of the most recent editions of the botanical manuals which include the whole of Michigan in their area, extensive changes have been made in the nomenclature and the generally accepted specific limitations among the members of their largest genus, *Carex*. To make this information available to the many students of the local flora in Michigan, it seems advisable to offer a modern treatment of the group.

A study of the collections in the principal available herbaria in the state has indicated that published records for many species from Michigan were based upon erroneous reports while, on the other hand, several species not heretofore known from the state can now be added to its flora. It is hoped, too, that the present treatment of the Michigan *Carices* will bring our knowledge of their distribution more nearly in line with their actual ranges.

The varied topography of the state, resulting in a diversity of habitats, and the range of latitude with its concomitant diversity in edaphic and climatic factors, presage a varied flora which is well borne out in the sedges. The total number of *Carices* now known from Michigan, including varieties and two distinctive forms, is 181. For the state of New York 188 species have been reported (H. D. House in N. Y. State Mus. Bull. no. 254, 1924) but, so far as known to the writer, this is the largest number recorded for any state and the known species from few states would equal the total represented from Michigan.

The distribution of the species within the state is of special interest. As would be expected in an area ranging in phytogeographic zones from Hudsonian to Appalachian, many of the sedges are distinctly boreal in their affinities and a other large group is as markedly austral. In addition to these a small Coastal Plain element (*C. Emmonsii*, *C. leptalea* var. *Harperi*, *C. exilis*, *C. seorsa*, *C. Longii* and *C. albolutescens*) is evident, and a few species appear to be confined to the proximity of the shores of the Great Lakes (*C. Crawei* and *C. Garberi*).

The definitely northern species, either restricted to the Upper Peninsula or having outposts in the northern counties of the Lower Peninsula are:

<i>C. canescens</i>	<i>C. Backii</i>	<i>C. pallescens</i>
<i>C. arcuata</i>	<i>C. scirpoidea</i>	<i>C. Houghtonii</i>
<i>C. gynocrates</i>	<i>C. concinna</i>	<i>C. angarae</i>
<i>C. interior</i> var. <i>heweenawensis</i>	<i>C. saltuensis</i>	<i>C. atratifformis</i>

<i>C. angustior</i>	<i>C. ormostachya</i>	<i>C. lenticularis</i>
<i>C. cephalantha</i>	<i>C. deflexa</i>	<i>C. aquatilis</i>
<i>C. Crawfordii</i>	<i>C. Rossii</i>	<i>C. gynandra</i>
<i>C. adusta</i>	<i>C. Knieskernii</i>	<i>C. Michauxiana</i>
<i>C. foenea</i>	<i>C. capillaris</i>	<i>C. Schweinitzii</i>

Of these some, such as *C. atratiformis*, *C. saltuensis*, *C. lenticularis*, *C. scirpoidea*, *C. capillaris*, *C. angustior* and *C. deflexa*, are wide ranging boreal plants while others, such as *C. Rossii*, *C. concinna*, *C. angarae* and *C. aquatilis*, in their present distribution are best developed in the far Northwest.

The southern species in the state, if the species ranging north to Saginaw Bay be included, are very nearly twice as numerous as the northern. Practically confined to the southernmost three tiers of counties are:

<i>C. Leavenworthii</i>	<i>C. Longii</i>	<i>C. Davisii</i>
<i>C. gravida</i> var. <i>Lunelliana</i>	<i>C. albulatensis</i>	<i>C. virescens</i>
<i>C. decomposita</i>	<i>C. leptalea</i> var. <i>Harperi</i>	<i>C. hyalinolepis</i>
<i>C. Crus-corvi</i>	<i>C. artitecta</i>	<i>C. Frankii</i>
<i>C. Howeii</i>	<i>C. platyphylla</i>	<i>C. typhina</i>
<i>C. festuacea</i>	<i>C. oligocarpa</i>	<i>C. squarrosa</i>

Extending northward to Saginaw Bay are:

<i>C. Muhlenbergii</i> var. <i>enervis</i>	* <i>C. Woodii</i>	<i>C. Sprengelii</i>
* <i>C. cephaloidea</i>	* <i>C. Caryeana</i>	<i>C. Swanii</i>
* <i>C. sparganioides</i>	* <i>C. digitalis</i>	* <i>C. hirsutella</i>
* <i>C. incompta</i>	* <i>C. laxiculmis</i>	<i>C. Haydenii</i>
* <i>C. normalis</i>	* <i>C. laxiculmis</i> var. <i>copulata</i>	<i>C. Emoryi</i>
* <i>C. molestia</i>	* <i>C. gracilescens</i>	<i>C. subimpressa</i>
* <i>C. alata</i>	* <i>C. granularis</i>	<i>C. altherodes</i>
* <i>C. muskingumensis</i>	* <i>C. conoidea</i>	* <i>C. trichocarpa</i>
* <i>C. Hitchcockiana</i>	* <i>C. grisea</i>	<i>C. Grayii</i>
* <i>C. hirtifolia</i>	<i>C. prasina</i>	* <i>C. lupuliformis</i>
* <i>C. tetanica</i>	<i>C. formosa</i>	

Noteworthy in this group is the large number of species (here indicated by an asterisk) whose northern limits appear to be demarked by the Grand River channel. Since this connective of glacial Lakes Saginaw and Chicago functioned as an outlet for a much longer time than any other channel in Michigan the apparent coincidence of the distributional limits of so many species with its course is at least suggestive that it may have been an important limiting factor. It would probably be precipitate at this time to ascribe much weight to glacial phenomena in influencing plant distribution in the state, because of the incompleteness of botanical exploration in Michigan, but that it is a factor which cannot be neglected in any definitive account of the state phytogeography is apparent from the present study. Seemingly corroborative evidence of this is found in the known distribution of *C. formosa* which coincides with the course of the Imlay outlet of glacial Lake Maumee.

In the distribution of the sedges in the state as a whole, disjunct ranges may be in some cases ascribed to the probability that the species are relicts. Such species are *C. tenuiflora*, *C. arcta*, *C. gynocrates*, *C. exilis* and *C. interior* var. *keweenawensis*. But in other instances it seems more likely that the apparent gaps are due to inadequate collecting. Thus among the thousands of collections reviewed for the present treatment no material whatever was found from Wexford, Missaukee, Kalkaska and Montmorency Counties and the amount

from the neighboring Crawford, Otsego, Oscoda and Ogemaw Counties was negligible. Other scattered counties which are rarely represented by collections are numerous, but this north-central portion of the Lower Peninsula seems to be the least known botanically of any extensive area in the state. It is hoped that the distribution maps included in this paper, in addition to establishing the known range of each species, will suggest the areas of the state most in need of further botanical field work.

Herbaria from which the Michigan collections of *Carex* were reviewed for the present study are indicated in citations by the following abbreviations:

- D—Herbarium of R. R. Dreisbach, Midland, Mich.
- G—Gray Herbarium, Cambridge, Mass.
- H—Herbarium of F. J. Hermann, Washington, D. C.
- Hn—Herbarium of C. R. and F. N. Hanes, Schoolcraft, Mich.
- K—Herbarium of the Catholic Junior College, Grand Rapids, Mich.
- M—Herbarium of the University of Michigan, Ann Arbor, Mich.
- ND—Herbarium of the University of Notre Dame, Notre Dame, Ind.
- NY—Herbarium of the New York Botanical Garden, New York, N.Y.
- S—Herbarium of Michigan State College, East Lansing, Mich.
- US—U. S. National Herbarium, Washington, D. C.

To the curators of these herbaria the writer is deeply grateful for the loan of material for study. Special thanks are due to Mr. and Mrs. C. R. Hanes for their painstaking cooperation in carefully exploring Kalamazoo County and adjoining areas for *Carices*. As may be seen from the citations many species are at present known in Michigan from their collections only.

Because of lack of space citations of collections are given for only the rarer sedges, generally those known from four collections or less, the distribution of the others being indicated by county in the maps. Nomenclatorial citations are included only for those species whose taxonomic status has changed since the publication of K. K. Mackenzie's monograph of the genus in *North American Flora* 18:1-478. 1931-35. Of the excluded species only those whose occurrence in the state seems plausible are included in the keys, and of the species which have been reported to occur in Michigan only those which were found to be actually represented by specimens in the herbaria have been credited to the state.

KEY TO THE SECTIONS OF MICHIGAN CARICES

Spike one.

Stigmas two; achenes lenticular.

- Pistillate spike without empty scales at the base; plants loosely stoloniferous.....11. DIOICAE, p. 17
- Pistillate spike with empty scales at the base; plants densely cespitose.....*C. exilis* in 12. STELLULATAE, p. 17

Stigmas three; achenes trigonous.

- Spikes gynaeandrous,¹ many-flowered; perigynia strongly inflated, sessile, not reflexed44. SQUARROSAE, p. 62
- Spikes androgynous² or dioecious; perigynia not inflated.
- Lower pistillate scales foliaceous; perigynia abruptly beaked.....16. PHYLLOSTACHYAE, p. 30
- Lower pistillate scales not foliaceous; perigynia not abruptly beaked.
- Perigynia pubescent; spikes dioecious18. SCIRPINAE, p. 36

¹ Pistillate flowers above, staminate at the base.

² Staminate flowers above, pistillate at the base.

- Perigynia glabrous; spikes androgynous.
 Perigynia slender-beaked, reflexed at maturity; pistillate scales deciduous40. ORTHOCERATES, p. 40
 Perigynia beakless, not reflexed; pistillate scales persistent15. POLYTRICHOIDEAE, p. 30
- Spikes more than one.
 A. Stigmas two; achenes lenticular.
 B. Lateral spikes sessile, short; terminal spike usually androgynous or gynae-
 candrous. (Subgenus *Vignea*.)
 Culms arising singly or few together from long-creeping rootstocks; peri-
 gynia not subterete.
 Heads ovoid, 0.5-1.2 cm. long; culms becoming decumbent and branch-
 ing; perigynia oblong-obovate, thick-plano-convex, 2.5-3.75 mm.
 long; plants of sphagnum bogs4. CHORDORRHIZAE, p. 8
 Heads elongate, 2-7 cm. long; culms not branching; not plants of
 sphagnum bogs.
 Perigynia wing-margined at least above; lowest spikes usually pistil-
 late, the middle staminate and terminal androgynous3. ARENARIAE, p. 7
 Perigynia not wing-margined; spikes all androgynous.
 Upper sheaths hyaline ventrally; perigynia not thin-margined, the
 beak not sharply bidentate1. DIVISAE, p. 7
 Upper sheaths green-striate ventrally; perigynia thin-margined
 above, the beak becoming bidentate2. INTERMEDIAE, p. 7
 Culms caespitose, the rootstocks occasionally somewhat prolonged with short
 internodes but not long-creeping (except sometimes in *C. disperma* of
 §*Disperma* which has subterete perigynia).
 Spikes androgynous, many-flowered; perigynia not subterete.
 Perigynia tapering into the beak or, if abruptly contracted, culms
 flaccid and flattening in drying8. VULPINAE, p. 13
 Perigynia abruptly contracted into the beak; culms not flaccid and not
 flattening in drying.
 Spikes few (generally 10 or fewer), usually greenish.....5. BRACTEOSAE, p. 8
 Spikes numerous, yellowish or brownish at maturity; leaf-sheaths
 often red-dotted ventrally.
 Perigynia plano-convex, thin, yellowish; bracts mostly much
 exceeding the spikes; leaf-sheaths usually transversely rugu-
 lose ventrally6. MULTIFLORAE, p. 12
 Perigynia thick-plano-convex or unequally biconvex, brown;
 bracts mostly shorter than the spikes; leaf-sheaths not trans-
 versely rugulose7. PANICULATAE, p. 12
 Spikes not androgynous or, if so, perigynia subterete and spikes only
 1-3-flowered.
 Spikes androgynous; perigynia subterete or unequally biconvex.....9. DISPERMAE, p. 15
 Spikes gynaeandrous; perigynia plano-convex.
 Perigynia with winged margins14. OVALES, p. 22
 Perigynia without winged margins, at most thin-edged.
 Perigynia 4.5-5.5 mm. long, narrowly lanceolate, appressed.....13. DEWEYANAE, p. 21
 Perigynia 1.8-4 mm. long.
 Perigynia thin-edged, spreading, ovoid, usually broadest below
 the middle12. STELLULATAE, p. 17
 Perigynia not thin-edged, ascending or appressed, elliptic.....10. HELEONASTES, p. 10
- BB. Lateral spikes peduncled or, if sessile, elongate; terminal spike usually
 staminate. (Subgenus *Eucarex*.)

- Style continuous with the achene, persistent, indurated; perigynia lustrous.45. VESICARIAE, p. 63
- Style articulated with the achene, at length deciduous; perigynia not lustrous.
- Lowest bract long-sheathing; perigynia pulverulent or golden-yellow at maturity22. BICOLORAE, p. 37
- Lowest bract sheathless or rarely short-sheathing; perigynia not pulverulent or golden-yellow.
- Achenes constricted in the middle; scales long-awned, 3-nerved.39. CRYPTOCARPAE, p. 58
- Achenes not constricted in the middle; scales not long-awned, 1-nerved38. ACUTAE, p. 55
- AA. Stigmas three; achenes trigonous.
- Perigynia pubescent or scabrous.
- Style continuous with the achene, persistent, indurated.
- Perigynia less than 1 cm. long; spikes cylindric.....43. PALUDOSAE, p. 61
- Perigynia 1 cm. long or longer; spikes globoseC. Grayii in 46. LUPULINAE, p. 65
- Style articulated with the achene, at length deciduous.
- Achenes closely enveloped by the perigynia; bracts sheathless or nearly so.
- Perigynia obtusely triangular or orbicular-triangular in cross-section; plant (except perigynia) glabrous17. MONTANAE, p. 30
- Perigynia sharply triangular in cross-section; plant pubescent20. TRIQUETRAE, p. 37
- Achenes not closely enveloped by the perigynia or, if so, the bracts strongly sheathing.
- Plants largely dioecious; many of the terminal spikes wholly pistillate.18. SCIRPINAE, p. 36
- Plants never dioecious; terminal spikes staminate or gynaeandrous.
- Bracts sheathing, their blades absent or rudimentary; achenes closely enveloped by the perigynia19. DIGITATAE, p. 36
- Bracts with well-developed blades.
- Bracts, at least the lower ones, long-sheathing.
- Beak of perigynium strongly bidentate34. HIRTAE, p. 52
- Beak of perigynium not strongly bidentate....24. LAXIFLORAE, p. 40
- Bracts sheathless or the lower short-sheathing.
- Perigynia scabrous35. ANOMALAE, p. 52
- Perigynia pubescent.
- Beak of perigynium strongly bidentate; styles long, slender; leaves septate-nodulose34. HIRTAE, p. 52
- Beak of perigynium at most shallowly bidentate; styles very short, thickish; leaves not septate-nodulose33. VIRESCENTES, p. 50
- Perigynia glabrous.
- Style not articulated, continuous with the achene, persistent, indurated.
- Perigynia subcoriaceous and firm43. PALUDOSAE, p. 61
- Perigynia membranaceous.
- Perigynia obconic or broadly obovoid, truncately contracted into the long, subulate beaks44. SQUARROSAE, p. 62
- Perigynia from lanceolate to ovoid or globose-ovoid, not truncately contracted.
- Perigynia lanceolate or ovoid-lanceolate, tapering into the beak.
- Perigynia many-nerved, slightly inflated, 3 mm. wide or less, yellowish-green; achenes 3.5 mm. long41. FOLLICULATAE, p. 58

- Perigynia ribbed, strongly inflated, ovoid-lanceolate, 3.5 mm. wide or more, green; achenes 5 mm. long. 46. LUPULINAE, p. 65
- Perigynia broader, abruptly contracted into the beak, usually strongly ribbed.
- Perigynia finely and closely ribbed 42. PSEUDO-CYPERI, p. 59
- Perigynia coarsely ribbed.
- Perigynia 7-10 mm. long; achenes 2-3 mm. long, 1.25-2.25 mm. wide. 45. VESICARIAE, p. 63
- Perigynia 10-20 mm. long; achenes 2.5-6 mm. long, 2-4 mm. wide 46. LUPULINAE, p. 65
- Style articulated with the achene, at length deciduous.
- Achenes strongly constricted at the base, rounded at the apex; lower pistillate scales bract-like 16. PHYLLOSTACHYAE, p. 30
- Achenes not strongly constricted at the base, apiculate; lower pistillate scales not bract-like.
- Lower bracts sheathless or very short-sheathing.
- Terminal spike gynaeandrous 37. ATRATAE, p. 53
- Terminal spike staminate (in *C. prasina* occasionally bearing a few perigynia); perigynia appressed or ascending; leaf-sheaths not septate-nodulose.
- Perigynia rounded and minutely beaked at the apex; pistillate spikes oblong, 1-2.5 cm. long. 36. LIMOSAE, p. 53
- Perigynia tapering into a beak nearly the length of the body; pistillate spikes linear, 2-6 cm. long *C. prasina* in 28. GRACILLIMAE, p. 45
- Lower bracts long-sheathing.
- Bracts bladeless or with rudimentary blades
- Leaf-blades filiform 21. ALBAE, p. 37
- Leaf-blades not filiform 24. LAXIFLORAE, p. 40
- Bracts with well-developed blades.
- Foliage, especially the sheaths, pubescent or puberulent.
- Perigynia beakless or short-beaked; terminal spike gynaeandrous (rarely staminate in *C. gracillima*) 28. GRACILLIMAE, p. 45
- Perigynia conspicuously beaked; terminal spike staminate. 29. SYLVATICAE, p. 47
- Foliage glabrous.
- Beak of perigynium bidentate.
- Pistillate spikes oblong-cylindric, on slender drooping peduncles; perigynia obliquely cut, at length bidentate 31. LONGIROSTRES, p. 49
- Pistillate spikes suborbicular to short-oblong, on short erect or ascending peduncles or sessile; perigynia equally bidentate 32. EXTENSAE, p. 49
- Beak of perigynium not bidentate, at most emarginate.
- Pistillate spikes short, oblong or linear, erect or, if drooping, either on long capillary peduncles or the perigynia sharply trigonous.
- Perigynia with few to many strongly raised nerves.
- Perigynia rounded at the base, suborbicular in cross-section, loosely enveloping the achenes. 25. GRANULARES, p. 43
- Perigynia tapering at the base, trigonous, closely enveloping the achenes.
- Rootstocks elongate, often producing long horizontal stolons 23. PANICEAE, p. 37

- Rootstocks not elongate, not producing long horizontal stolons24. LAXIFLORAE, p. 40
- Perigynia with numerous fine impressed nerves.
Perigynia tapering at the base, constricted at the apex, obtusely triangular in cross-section, closely enveloping the achenes26. OLIGOCARPAE, p. 44
- Perigynia rounded at both ends, orbicular to orbicular-triangular in cross-section27. GRISEAE, p. 45
- Pistillate spikes elongate, linear to cylindric; on slender peduncles, the lower usually drooping; perigynia not sharply trigonous.
Perigynia beakless or short-beaked; terminal spike gynae-candrous28. GRACILLIMAE, p. 45
- Perigynia conspicuously beaked; terminal spike staminate.
Culms strongly reddish-tinged at the base, aphyllopodic.³29. SYLVATICAE, p. 47
- Culms not reddish-tinged at the base, phyllopodic.⁴
Pistillate spikes slender, 3-4 mm. wide, few-flowered; perigynia 2.5-4 mm. long.....30. CAPILLARES, p. 49
- Pistillate spikes stout, 8-10 mm. wide, many-flowered; perigynia 5-6 mm. long.....31. LONGIROSTRES, p. 49

Section 1. DIVISAE

1. CAREX PRAEGRACILIS W. Boott

C. camporum Mack.; *C. marcida* Boott

A western species, chiefly of prairies. In Michigan known from a single locality: low sandy depression in jack pine plain, Eagle Harbor, Keneenaw County, *M. L. Fernald & A. S. Pease* 3158 (July, 1934) (G, M) and *F. J. Hermann* 7763 (July 2, 1936) (H, M. NY, S, US). Reported by Beal (1908) as having been collected on Thunder Bay Island, Port Huron, by C. K. Dodge, but specimens to confirm this report could not be found.

Northern Mich., Man. and Iowa to Yukon, B. C. and Calif., southw. to Tex. and Mex.; S. A.

Section 2. INTERMIDIAE

2. CAREX SARTWELLI Dewey

Frequent in the southern half of the Lower Peninsula; locally plentiful in calcareous marshes and on marshy borders of lakes especially in marly soils. In the Upper Peninsula known only from a collection by C. K. Dodge from "near Manistique" (June 29, 1915) (M).

Ont. and w. N. Y. to B. C., southw. to Ill., Mo., Nebr. and Colo.

Section 3. ARENARIAE

3. CAREX SICCATA Dewey

In dry open sandy or gravelly soils. Frequent in the southern half of the Lower Peninsula; otherwise known only from one locality: bare, gravelly summit of West Bluff, 3½ miles west of Copper Harbor, Keweenaw County, *M. L. Fernald & A. S. Pease* 3157 (July 4, 1934) (G, M) and *F. J. Hermann* 7527 (June 18, 1936) (H, NY).

Maine to Wash. and Mack., southw. to N. J., Ind., Nebr. and Ariz.

³ Basal sheaths bladeless or with rudimentary blades.

⁴ Basal sheaths with well-developed blades.

Section 4. CHORDORRHIZAE

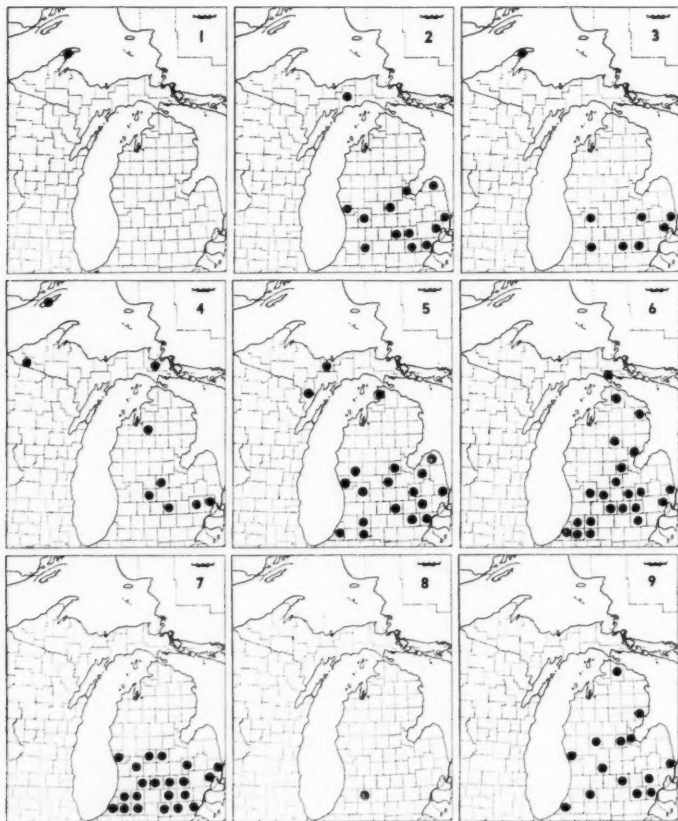
4. CAREX CHORDORRHIZA L. f.

In sphagnum bogs and on peaty borders of lakes. Infrequent.

Lab. and Newf. to Keewatin, southw. to N. Y., Ind., Iowa and Sask.; Eurasia.

Section 5. BRACTEOSAE

A. Sheaths tight, inconspicuously or not at all mottled with green and white or septate-nodulose dorsally (except sometimes in *C. Leavenworthii*); leaf-blades 1-4.5 mm. wide.



1. *C. praegracilis* W. Boott; 2. *C. Sartwellii* Dewey; 3. *C. siccata* Dewey; 4. *C. chordorrhiza* L. f.; 5. *C. rosea* Schkuhr; 6. *C. convoluta* Mack.; 7. *C. cephalophora* Muhl.; 8. *C. Leavenworthii* Dewey; 9. *C. Muhlenbergii* Schkuhr.

- Perigynia distended and spongy at the base, usually widely spreading or reflexed at maturity.
- Beaks of perigynia smooth, scarcely exceeding the acuminate, deciduous scales. (See excluded species no. 1.)..... *C. retroflexa*
- Beaks of perigynia minutely serrulate, much exceeding the obtuse or somewhat acute, persistent scales.
- Stigmas long, slender, usually not twisted, light reddish; perigynium tapering into the beak; leaf-blades 1-2 mm. wide.....5. *C. rosea*
- Stigmas short, stout, strongly twisted or contorted, deep red; perigynium abruptly contracted into the beak; leaf-blades 1.5-3 (averaging 2.5) mm. wide.....6. *C. convoluta*
- Perigynia not distended and spongy at the base, mostly ascending.
- Inflorescence ovoid or oblong-ovoid; spikes densely capitate.
- Scales much shorter than the bodies of the perigynia.
- Perigynia broadest below the middle, round-tapering at the base, with ventrally raised margins; beaks long, serrulate.....7. *C. cephalophora*
- Perigynia broadest at the truncate-cordate base, flat ventrally; beaks short, smooth.....8. *C. Leavenworthii*
- Scales from little shorter to longer than the bodies of the perigynia.....9a. *C. Muhlenbergii* var. *enervis*
- Inflorescence oblong or linear-oblong to elongate and interrupted; spikes not capitate.
- Perigynia strongly nerved and low-convex ventrally, the margins usually slightly raised.....9. *C. Muhlenbergii*
- Perigynia nerveless or nerved only at the base ventrally, the margins not raised at maturity.....9a. *C. Muhlenbergii* var. *enervis*
- AA. Sheaths loose, mottled with green and white and usually septate-nodulose dorsally; leaf-blades 4.5-8 (in *C. aggregata* rarely only 3) mm. wide.
- Perigynia not deep green at maturity, with border raised ventrally only above the middle, the beak one-fourth to one-third the length of the broadly ovate or suborbicular body or, if longer, the ventral suture deep; spikes approximate in a cylindric or ovoid head.....10. *C. gravida* var. *Lunelliana*
- Perigynia deep green, the beak one-third the length of the ovate body or more or, if rarely shorter, the ventral suture shallow.
- Mature perigynia membranaceous, flat ventrally; leaf-blades 3-7 mm. wide; spikes approximate or the lower separate.
- Scales acute or somewhat obtuse, half the length of the bodies of the perigynia; stigmas short; sheaths truncate at the mouth, the lower transversely rugulose; perigynia narrowly ovate or elliptic with narrow, gradually contracted beak; culms often slightly winged.....11. *C. cephaloidea*
- Scales acuminate or short cuspidate (rarely merely acute), about the length of the perigynia; stigmas long and slender; sheaths concave at the mouth, usually not at all transversely rugulose; culms sulcate and white-striate up to the inflorescence, their angles usually smooth.....12. *C. aggregata*
- Mature perigynia subcoriaceous, ovate, with border raised ventrally to the base, abruptly contracted into a short, stout beak; culms sulcate and white-striate only below, their angles serrulate and minutely winged or thin-edged up to the inflorescence; leaf-blades 5-10 mm. wide; lower sheaths usually transversely rugulose; lower spikes usually separate; stigmas short, stout; scales short, blunt to acute.....13. *C. sparganioides*

5. CAREX ROSEA Schkuhr

C. rosea var. *minor* Boott

In both dry and moist deciduous woods. Common in the southern half of the Lower Peninsula, absent from the jack pine plains and rare northward.

N. S. to N. Dak., southw. to Ga. and La.

6. *CAREX CONVOLUTA* Mack.

C. rosea of authors.

In deciduous woods, generally in rich soils. Very common in the southern half of the Lower Peninsula, becoming infrequent to rare northward.

N. S. to Man., southw. to Ala., Tenn. and Ark.

7. *CAREX CEPHALOPHORA* Muhl.

Apparently restricted to the southern half of the Lower Peninsula. Very common in more or less open woods and thickets; occasional in fields.

Maine to Man., southw. to Fla. and Tex.

8. *CAREX LEAVENWORTHII* Dewey

A southern species reaching the northern limit of its range in southern Michigan. Known only from Kalamazoo County: sterile soil, Cooper's Glen, C. R. & F. N. Hanes 3557 (June 8, 1937) (Hn) and, roadside in village, Schoolcraft, C. R. & F. N. Hanes 199 (June 11, 1939) (Hn, M).

Southern N. J., sw. Ont. and Iowa to Fla. and Tex.

9. *CAREX MUHLENBERGII* Schkuhr

Frequent in the Lower Peninsula, becoming common in the southern half.

In sandy soils in the open, on dunes and in dry open oak and aspen woods.

Maine to Minn., southw. to Fla. and Tex.

9a. *CAREX MUHLENBERGII* var. *ENERVIS* Boott

C. plana Mack.

Open sandy habitats. Frequent in the southern half of the Lower Peninsula.

Maine to Nebr., southw. to Ala. and Tex.

10. *CAREX GRAVIDA* Bailey var. *LUNELLIANA* (Mack.) Hermann (Amer. Midl. Nat. 17:857. 1936.)

C. Lunelliana Mack.

A southwestern sedge known in the state only from a collection by P. E. Hebert: Bertrand, Berrien County (June 14, 1931) (ND). It is a plant of dry prairie habitats.

Mich., Ind. and Iowa to Tex. and N. Mex.

11. *CAREX CEPHALOIDEA* Dewey

Frequent in the southern half of the Lower Peninsula. Its preferred habitat is rich woods but occasionally it occurs in moist fields.

Immature specimens of *C. alopecoidea* (§ *Vulpinae*) which simulate *C. cephaloidea* may be distinguished by their green-centered acuminate to aristate pistillate scales. The pistillate scales of *C. cephaloidea* are shorter (not over half the length of the bodies of the perigynia), hyaline throughout except for the faint midrib and obtuse to merely acute.

N.B. to Minn., southw. to N. J. and Ill.

12. *CAREX AGGREGATA* Mack.

Known only from Kalamazoo County: lawn in village of Schoolcraft, C. R.

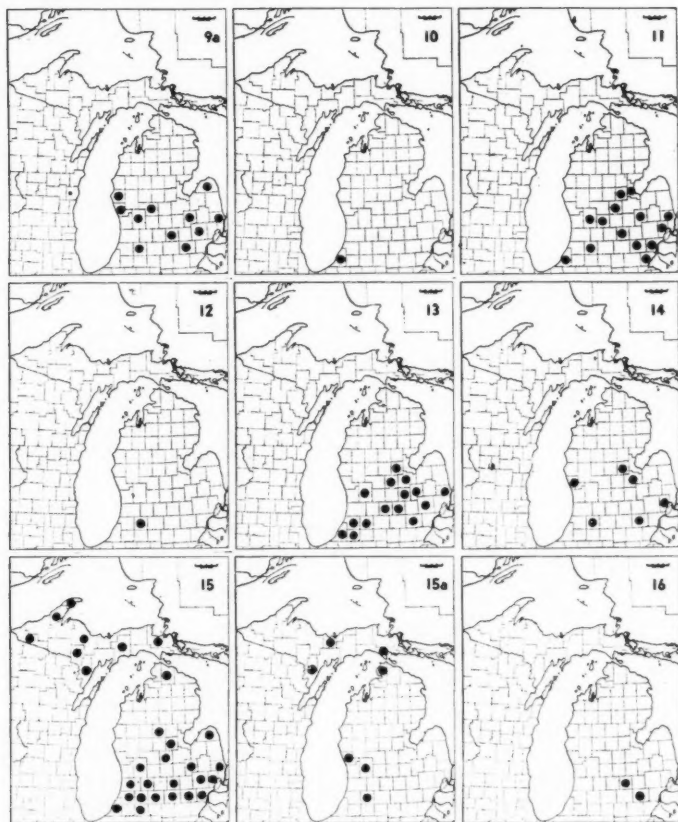
& F. N. Hanes 1284 (June 6, 1934) (Hn), and F. J. Hermann 9060 (July 10, 1937) (H, NY); roadside, Schoolcraft, C. R. & F. N. Hanes 209 (June 11, 1939) (M). Probably introduced.

N. J. to D. C., westw. to Kans. and Okla.

13. *CAREX SPARGANOIDES* Muhl.

Very common in rich woods and thickets in the southern half of the Lower Peninsula.

Que. to S. Dak., southw. to Va., Ky. and Kans.



9a. *C. Muhlenbergii* var. *enervis* Boott; 10. *C. grvida* var. *Lunelliana* (Mack.) Hermann; 11. *C. cephaloidea* Dewey; 12. *C. aggregata* Mack. 13. *C. sparganioides* Muhl. 14. *C. annectens* Bickn.; 15. *C. vulpinoidea* Michx.; 15a. *C. vulpinoidea* var. *pycnocephala* Hermann; 16. *C. decomposita* Muhl.

Section 6. MULTIFLORAE

Beak of perigynium much shorter than the body; perigynium subcoriaceous; leaves usually shorter than the culms.

Perigynia mostly broadest at the base, usually nerved dorsally, 2 mm. or more wide; beak of perigynium prominent, conspicuously cleft.....14. *C. annectens*

Perigynia mostly broadest at or below the middle, nerveless dorsally; usually less than 2 mm. wide; beak of perigynium very small, obscurely cleft; heads generally shorter and denser. (See excluded species no. 4).....

.....*C. annectens* var. *xanthocarpa*
Beak of perigynium about equaling the body; perigynium membranaceous; leaves normally exceeding the culms.

Perigynia ovate, the body corky-margined to the base, contracted into the beak....

.....15. *C. vulpinoidea*

Perigynia narrowly lanceolate, the body thin-edged and not at all corky-margined, tapering gradually into the beak; teeth of perigynium almost obsolete; plant low, densely cespitose; leaves narrow, rigid; inflorescence short, broad and congested

.....15a. *C. vulpinoidea* var. *pycnocephala*

14. *CAREX ANNECTENS* Bickn.

C. selacea var. *ambigua* (Barratt) Fern.

Frequent in the southern half of the Lower Peninsula in marshes and along low open roadsides or roadside ditches. Represented from the Upper Peninsula by a single collection by H. T. Darlington: low ground, Porcupine Mountains, Ontonagon County (August 1923) (S).

Maine to Wisc., southw. to Tex. and Fla.

15. *CAREX VULPINOIDEA* Michx.

Very common throughout the state. It is especially plentiful in roadside ditches but is found in wet habitats of all types particularly in open situations.

Newf. to B. C., southw. to Fla., Tex., Ariz. and Oreg.

15a. *CAREX VULPINOIDEA* var. *PYCNOCEPHALA* Hermann (Rhodora 38:363. 1936.)

Frequent on sandy and marshy borders of lakes. The type collection is from the sandy shore of Lake Michigan, Big Stone Bay, Emmet County, F. J. Hermann 6408 (August 4, 1934) (G, H).

Ont., Mich. and Minn.; probably elsewhere on sandy shores of the Great Lakes.

Section 7. PANICULATAE

Leaf-blades 3-8 mm. wide; perigynia very abruptly short-beaked, tapering at the base; inflorescence usually 8-15 cm. long, obviously branched.....16. *C. decomposita*

Leaf-blades 1-3 mm. wide; perigynia tapering or contracted into the beak, rounded or truncate at the base; inflorescence 2.5-5 (8) cm. long, obscurely branched.

Sheaths not copper-colored at the mouth; head little interrupted; perigynia 2-2.5 mm. long, convex ventrally, lustrous; not concealed by the scales.....

.....17. *C. diandra*

Sheaths copper-colored at the mouth; head interrupted; perigynia 2.5-3.5 mm.

long, flat ventrally, dull, nearly concealed by the scales.....18. *C. prairea*

16. *CAREX DECOMPOSITA* Muhl.

Rare and very local. A collection in the University of Michigan Herbarium is labelled merely Ann Arbor, without collector or date. In the Michigan

State College Herbarium is a sheet with the data, "Lansing, Mich., June 17, 1887" and a collection by C. F. Wheeler from "cat hole" on College Farm, East Lansing, Ingham County, July 17, 1891. Specimens to corroborate Beal's report (1904) for Hubbardston could not be located. Although it occurs in various rich swampy situations its choice habitats seem to be on logs in ponds and at the bases of stumps or trees in swamps.

N. Y. to Mich., southw. to Fla., La. and Mo.

17. *CAREX DIANDRA* Schrank.

C. teretiuscula Good.

Frequent throughout. It occurs in swampy and boggy habitats especially on boggy or marly borders of lakes and occasionally on wet sandy beaches.

Newf. to Alaska, southw. to N. J., Ind. and Colo.; also in Eurasia.

18. *CAREX PRAIREA* Dewey

C. diandra var. *ramosa* (Boott) Fern.; *C. teretiuscula* var. *prairea* (Dewey) Britt.

Frequent to fairly common in the southern half, and infrequent in the northern counties, of the Lower Peninsula. It is found in marshes, swamps and swales and on borders of streams and lakes.

Que. to Sask., southw. to N. J., Ind., Iowa and Nebr.

Section 8. VULPINAЕ

Perigynium tapering into the beak, the body strongly nerved ventrally or perigynium very long beaked.

Perigynium 4-6 mm. long, rounded at the base, strongly nerved ventrally, the beak 1-2 times the length of the body; sheaths not dotted with purple ventrally.

Sheaths not thickened at the mouth, cross-rugulose ventrally, easily broken, prolonged upward at the mouth 19. *C. stipata*

Sheaths thickened (often cartilaginous) at the mouth, rarely cross-rugulose ventrally, not easily broken, concave or truncate at the mouth 20. *C. laevivaginata*

Perigynium 6-7 mm. long, abruptly enlarged below into a disc-like base, obscurely nerved ventrally except at the base, the beak 2-3 times the length of the body; sheaths dotted with purple ventrally. 21. *C. Crus-corvi*

Perigynium contracted into a beak not longer than the body, the body nerveless ventrally except sometimes at the base.

Sheaths cross-rugulose ventrally; spikes green; perigynium broad, usually strongly nerved dorsally, the beak generally about half the length of the body. (See excluded species no. 5.) *C. conjuncta*

Sheaths not cross-rugulose ventrally; spikes yellowish or tawny at maturity; perigynium narrow, faintly nerved dorsally, the beak about the length of the body 22. *C. alopecoidea*

19. *CAREX STIPATA* Muhl.

Very common throughout the state. In wet habitats of all types especially in the open.

Newf. to Alaska, southw. to N. C., Tenn., Kans., N. Mex. and Calif.

20. *CAREX LAEVIVAGINATA* (Kükenth) Mack.

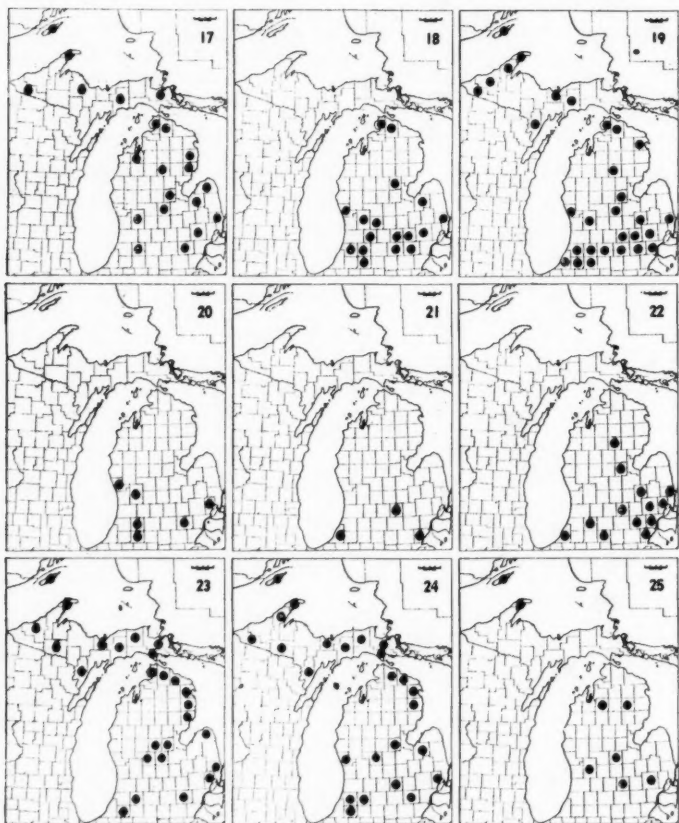
Apparently confined to the southern half of the Lower Peninsula. Frequent

in swamps and on borders of streams in woods in the two southernmost tiers of counties; infrequent northward.

Mass. to Minn., southw. to Fla. and Mo.

21. *CAREX CRUS-CORVI* Shuttlw.

Very rare. A southern species of low woods known in Michigan from three collections: low banks of River Raisin, 3 miles east of Dundee, Monroe County, C. F. Wheeler (June 11, 1890) (S); Reform School Marsh, near Lansing, Ingham County, C. F. Wheeler & W. J. Beal (July 4, 1892) (M, S); and



17. *C. diandra* Schrank; 18. *C. prairea* Dewey; 19. *C. stipata* Muhl.; 20. *C. laevivaginata* (Küken.) Mack.; 21. *C. Crus-corvi* Shuttlw.; 22. *C. alopecoidea* Tuckerm.; 23. *C. disperma* Dewey; 24. *C. trisperma* Dewey; 25. *C. tenuiflora* Wahl.

flood plain — low place in Warren Woods, Berrien County, *C. Billington* (July 29, 1919) (M).

Tenn. southw. to Fla. and Tex.; in the Mississippi Valley from Ohio, s. Mich., s. Minn. and e. Nebr. to La.

22. CAREX ALOPECOIDEA Tuckerm.

C. alopecoidea var. *sparsispicata* Desv.

Frequent to fairly common in the southern counties, becoming rare north of the Saginaw River Valley. It is partial to swampy meadows and marshes, occurring less frequently on river banks, flood plains and in low woods. The specimen forming the basis for the report by Brown (1937) from Isle Royale is *C. diandra*.

Que. to Minn., southw. to N. J. and Iowa.

Section 9. DISPERMAE

23. CAREX DISPERMA Dewey

C. tenella Schkuhr

Frequent throughout, becoming common in the northern counties of the Lower Peninsula and in the Upper Peninsula. In bogs, swamps and wet woods, often in sphagnum and usually in shade; best developed in Thuja bogs.

Newf. to Yukon, southw. to N. J., Ind., N. Mex. and Calif.; also in Eurasia.

Section 10. HELEONASTES

Lowest bract bristle-like, many times longer than its spike; spikes 1-5-flowered, widely separate; perigynia 3-3.5 mm. long 24. *C. trisperma*

Lowest bract much shorter; spikes several- to many-flowered, the upper ones approximate.

Perigynia 3-3.5 mm. long, beakless 25. *C. tenuiflora*

Perigynia 2-3 mm. long, apiculate to strongly beaked.

Perigynia broadest near the base, the conspicuous beak strongly serrulate.....

..... 28. *C. arcta*

Perigynia broadest near the middle; beak short, smooth.

Perigynia distinctly short-beaked, loosely spreading; leaves green, 1-2.5 mm.

wide 26. *C. brunnescens*

Perigynia apiculate, appressed-ascending; leaves glaucous, 2-4 mm. wide.

Spikes 6-10 mm. long, approximate or the lowest rarely 1.5 cm. apart;

perigynia 2.3-3 mm. long 27. *C. canescens*

Spikes 6-12 mm. long, remote, the lowest 2-4 cm. apart; perigynia

2.3-3 mm. long 27a. *C. canescens* var. *disjuncta*

Spikes 4-7 mm. long, subapproximate or remote; perigynia barely 2 mm.

long 27b. *C. canescens* var. *subuloliacea*

24. CAREX TRISPERMA Dewey

Common throughout the state in acid soils of swampy woods and bogs. It is especially frequent in arbor vitae, black spruce and tamarack bogs, generally in sphagnum and growing in deep shade.

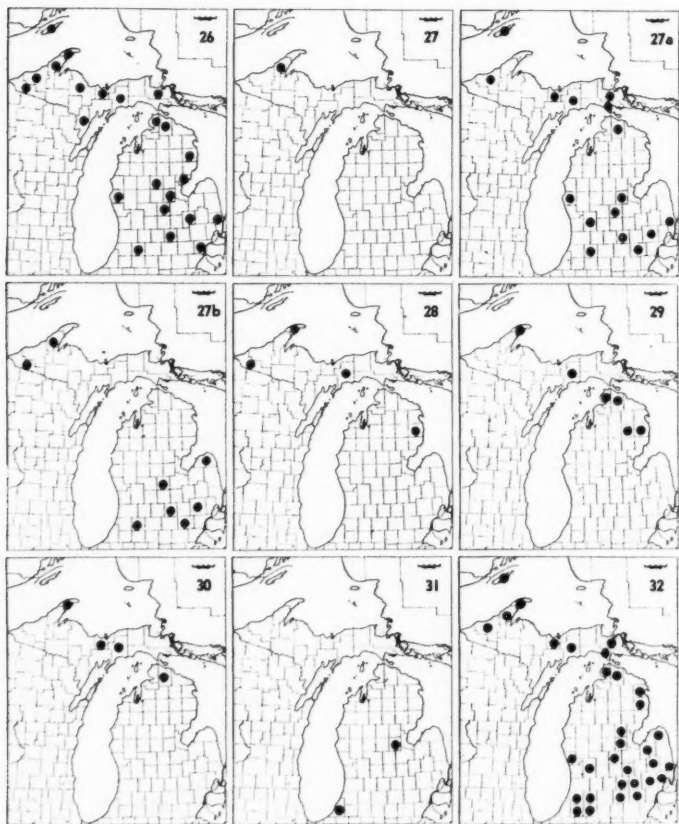
Newf. to Sask., southw. to Md., Ill. and Minn.

25. CAREX TENUIFLORA Wahl.

Infrequent and very local. A northern species probably reaching the south-

ern limit of its range in Ingham and Oakland Counties. It should be better represented from the Upper Peninsula than the records indicate, because of the frequency of its preferred habitat there, and the paucity of records is doubtless due in part to its local nature and to the fact that so few of the counties have been intensively explored botanically. It is found in cold sphagnum bogs, generally in shade under arbor vitae, black spruce or tamarack.

Lab. and Newf. to Yukon and s. Alaska, southw. to Maine, Mich. and Minn.; also in Eurasia.



26. *C. brunnescens* (Pers.) Poir.; 27. *C. canescens* L.; 27a. *C. canescens* var. *disjuncta* Fern.; 27b. *C. canescens* var. *subulolicea* Laestad.; 28. *C. arcta* Boott; 29. *C. gynocrates* Wormsk.; 30. *C. exilis* Dewey; 31. *C. scorsa* Howe; 32. *C. interior* Bailey.

26. CAREX BRUNNESCENS (Pers.) Poir.

C. brunnescens var. *gracilior* Britt.

Common in the Upper Peninsula, becoming less frequent southward and probably absent from the southernmost tier of counties. It prefers acid soils in bogs, swampy woods and boggy thickets.

Greenl., Lab., and Newf. to Alaska, southw. to N. J. (in the mts. to N. C.), Colo., and Wash.; also in Eurasia.

27. CAREX CANESCENS L.

Material of this boreal sedge has been seen from only one locality: in sphagnum and shallow water in a Chamaedaphne bog $\frac{1}{2}$ mile northeast of Laurium, Houghton County, F. J. Hermann 265 and 7598 (June 14, 1926 and June 21, 1936) (H, NY). The species has been frequently reported from all parts of the state but all reports are referable to one of the two following varieties.

Lab. to B. C., locally southw. to Conn. and n. Mich.; also in Eurasia.

27a. CAREX CANESCENS var. DISJUNCTA Fern.

Fairly common in bogs, in acid soils in swampy woods and thickets and on shaded borders of lakes and streams.

Lab. to Wisc., southw. to Pa. and Ind.

27b. CAREX CANESCENS var. SUBLOLIACEA Laestad.

Frequent in habitats of the preceding variety.

28. CAREX ARCTA Boott

Rare in swampy open habitats in northern Michigan. In the Lower Peninsula it has been found but once: swampy woods, Alcona County, H. T. Darlington (July 18, 1918) (S).

Lab. to B. C., southw. locally to Conn. and Ind.

Que. and N. B. to B. C., southw. to Mass., N. Y., Minn. and n. Calif.

Section 11. DIOICAE

29. CAREX GYNOCRATES Wormsk.

C. Redowskyana C. A. Mey.

Infrequent in sphagnum bogs in northern Michigan. Often locally plentiful but its stations are widely scattered. Its scarcity cannot be due to lack of favorable habitats as these are plentiful throughout the Upper Peninsula.

Greenl. to Yukon, southw. to N. Y., Mich., Colo. and B. C.; also in Siberia.

Section 12. STELLULATAE

Spike one (sometimes a small additional one at the base); leaf-blades rigid. 30. *C. exilis*
Spikes more than one; leaf-blades not rigid.

Perigynium broadest near the middle, strongly nerved both ventrally and dorsally,
the beak smooth.....31. *C. scorsa*

Perigynium broadest at the base, the beak serrulate.

Perigynia 2.25-3.25 mm. long, the beak shallowly bidentate.

Leaf-blades 0.25-1 mm. wide, lax, widely spreading; perigynia broadly

- ovate, deep green, strongly nerved ventrally, the beak with ventral false suture conspicuous; anthers 1-1.5 mm. long; scales sub-acute....33. *C. Howei*
- Leaf-blades 1-3 mm. wide, erect-ascending; perigynia ovate to oval or oblong-ovate, brownish or tawny, the beak with ventral false suture inconspicuous; anthers 1 mm. or less long.
- Perigynia plano-convex or concavo-convex, ovate to oblong-ovate, coriaceous, inconspicuously nerved ventrally toward the base, the beak short, less than half the length of the body; pistillate scales very obtuse, green with broad white-hyaline margins32. *C. interior*
- Perigynia unequally biconvex, very plump, narrowly ovate or oval, membranaceous, conspicuously nerved ventrally especially toward the base, the beak half the length of the body, narrower and longer than in the species; pistillate scales acute, hyaline throughout32a. *C. interior* var. *keweenawensis*
- Perigynia 2.75-4.75 mm. long, the beak deeply bidentate.
- Perigynia deep green at maturity, strongly nerved ventrally, the body very broadly ovate or suborbicular with raised margins, the beak less than half the length of the body, the teeth short, straight, rigid....34. *C. incompta*
- Perigynia stramineous to brown at maturity, nerveless to lightly nerved ventrally, the body ovate to lanceolate (occasionally broadly ovate in *C. sterilis*).
- Staminate flowers terminal, basal, or in separate spikes; margin of perigynium slightly if at all raised, setulose-serrulate toward the beak; beak of perigynium half the length of the body or more, the teeth broad, largely hyaline and soft, often bent or twisted; scales chestnut-brown, with lustrous white margins35. *C. sterilis*
- Staminate flowers mostly at the base of the terminal spikes; margin of perigynium serrulate toward the beak, the teeth short, stiff; scales yellowish-brown tinged, with narrow hyaline margin.
- Mature perigynia lanceolate, nerveless or impressed-nerved toward the base ventrally, the beak remotely low-serrulate, more than half the length of the body; achenes much longer than wide....36. *C. angustior*
- Mature perigynia ovate, with raised nerves ventrally; the beak strongly serrulate, much shorter than the body; achenes about as wide as long.
- Perigynia 2.75-3.3 mm. long, the beak about a third the length of the body, the teeth triangular; scales somewhat obtuse to acute.37. *C. laricina*
- Perigynia 3.5-4 mm. long, the beak about half the length of the body, the teeth subulate; scales acute to somewhat cuspidate38. *C. cephalantha*

30. CAREX EXILIS Dewey

Known in Michigan from five localities: 4 miles northwest of Clifton, Keweenaw County, *O. A. Farwell* 389 (June 20, 1886) (M, S); in sphagnum in open arbor vitae-black spruce bog, southeast of Eagle Harbor, Keweenaw County, *O. A. Farwell* 6629 (June 29, 1923) (H) and *F. J. Hermann* 7986 (July 13, 1936) (H, M, NY, S, US); open marshy ground on margin of Howe's Lake near Peter White Camp, Alger County, *C. K. Dodge* (June 30, 1916) (M); muskeg near Walsh, Schoolcraft County, *M. L. Fernald & A. S. Pease* 3165 (July 2, 1934) (G, M); and, on edges of spruce islands, Little Lake Sixteen bog, Cheboygan County, *L. H. Harvey* 699 (July 29, 1938) (M).

Lab. to Del., mostly near the coast; locally inland in Vt., N. Y., N. J., Ont., Mich. and Minn.

31. CAREX SEORSA Howe

C. roseoides Howe.

Very rare in wet woods and swamps. The three known collections are: Buchanan Swamp, Berrien County, P. E. Hebert (May 30, 1930) (ND); woods on bank of Tittabawassee River, 2 miles west and 1 mile north of Midland, Midland County, R. R. Driesbach 6790 (June 10, 1930) (D, H, M); and, woods 1 mile south and 1 mile west of Midland, R. R. Driesbach 7974 (June 6, 1934) (D).

Mass. to Ga., locally westw. to Mich. and Ind.

32. CAREX INTERIOR Bailey

C. scirpoides Schkuhr in part, not *C. scirpoidea* Michx.

Common in swamps, bogs, peaty meadows and on marshy banks of streams and lakes. It has a wide range of habitats, occurring indiscriminately in acid or strongly alkaline soils and although more commonly in open situations it is frequent in shady thickets and even in dark arbor vitae bogs. This diversity of habitat is probably responsible, at least in part, for the variability of the species.

Newf. to B. C., southw. to Pa., Ind., Kans., Chihuahua and Calif.

32a. CAREX INTERIOR var. KEWEENAWENSIS Hermann*

Known only from the type collection in sphagnum in arbor vitae bog, south-east of Eagle Harbor, Keweenaw County, F. J. Hermann 7985 (July 13, 1936) (G (TYPE), H, M, ND, NY, US).

This distinctive variant in its acute pistillate scales and the ventral nerving of the perigynia, resembles *C. Howe* but the perigynia are narrower than in that species, almost elliptic-ovate rather than deltoid-ovate, the anthers (0.7 mm.) are shorter and the leaves (1-1.75 mm. wide) are broader. The general shape of the perigynium is suggestive of that of the eastern *C. Josselynii* Fern. except that the beak is much narrower, and in the latter species the ventral nerves are conspicuous even on the beak instead of being pronounced only on the lower half of the perigynium body.

The failure of this variety to turn up among the other collections of *C. interior* studied (amounting to approximately 150 from Michigan and adjacent areas) suggests that it is an endemic of extremely localized distribution similar to *Chamaerhodos Nuttallii* var. *keweenawensis* Fern. and *Arnica Whitneyi* Fern. which, so far as known, are also confined to Keweenaw County (cf. Fernald, *Critical Plants of the Upper Great Lakes Region of Ontario and Michigan*, Rhodora 37:197-222, 238-262, 272-301, 324-341. 1935).

33. CAREX HOWEI Mack.

C. interior var. *capillacea* Bailey; *C. scirpoides* var. *capillacea* (Bailey) Fern.

A very local species known in Michigan from only two collections from Kalamazoo County: low ground in Prairie Ronde Township, 6 miles south-

* *Carex interior* Bailey var. *keweenawensis* var. nov. A varietate typica differt perigyniis anguste ovatis vel ovalibus haud oblongibus, pinguissimis, membranaceis, ventraliter nervosis, rostro quam corpore dimidio brevior, squamis haud marginatis omnino hyalinis.

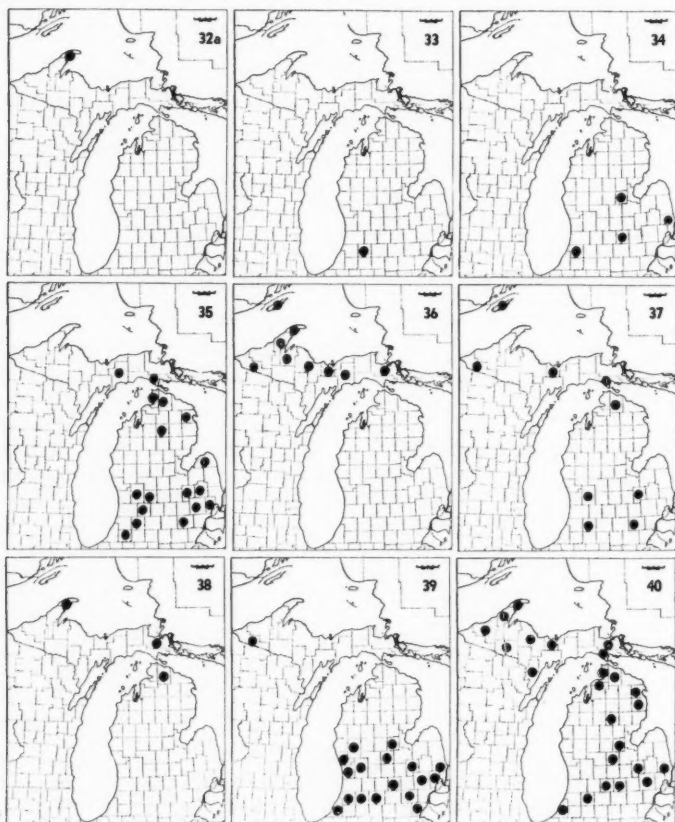
west of Schoolcraft, C. R. & F. N. Hanes 666 (May 29, 1936) (H, Hn) and, northeast of Goose Lake, C. R. & F. N. Hanes (June 25, 1938) (Hn).

N. S. to Fla. and La., westw. locally to Mich. and Ind.

34. *CAREX INCOMPERTA* Bickn.

C. stellulata var. *excelsior* Fern.

Infrequent to rare in swamps and moist thickets in the southern half of the Lower Peninsula. The report for Isle Royale (Brown, 1937) is based upon a specimen of *C. laricina*.



32a. *C. interior* var. *heweenawensis* Hermann; 33. *C. Howei* Mack.; 34. *C. incomperta* Bickn.; 35. *C. sterilis* Willd.; 36. *C. angustior* Mack.; 37. *C. laricina* Mack.; 38. *C. cephalantha* (Bailey) Bickn.; 39. *C. bromoides* Schkuhr; 40. *C. Deweyana* Schwein.

Mass. and N. Y. to Mich. and Ind., south. to Fla. and Tex.

35. CAREX STERILIS Willd.

C. scirpoides Schkuhr, in part.

Fairly common in the southern counties, becoming infrequent northward and rare in the Upper Peninsula. It occurs in swamps, boggy meadows and marshes, on borders of lakes and ponds, and, less frequently, in beach pools on the dunes.

Newf. to Minn., southw. to N. J., Pa. and Ill.

36. CAREX ANGUSTIOR Mack.

C. stellulata var. *angustata* Carey

Apparently restricted in Michigan to the Upper Peninsula where it is frequent to locally common in bogs, marshy thickets and wet, sandy, open habitats.

A specimen in the University of Michigan Herbarium (*C. A. Davis*, June 1, 1895) bears the label "Alma, Gratiot County," but the accuracy of the locality data is questionable.

Newf. to Wash., southw. to N. C. (in the mountains), Wyo. and Calif.

37. CAREX LARICINA Mack.

Frequent but local in bogs and in swampy and marshy habitats, chiefly in the open.

Ont. and Pa. to Wisc., southw. to Ind.

38. CAREX CEPHALANTHA (Bailey) Bickn.

C. sterilis var. *cephalanthia* Bailey

Known in Michigan from four collections: swampy west side of North Fishtail Bay, Douglas Lake, Cheboygan County, *L. E. Smith* 91 (July 23, 1917) (M); wet, marshy ground near Eckerman, Chippewa County, *C. K. Dodge* (June 14, 1914) (M); larch swamp near Emerson, Chippewa County, *M. L. Fernald & A. S. Pease* 3167 (July 1, 1934) (G, M); and, moist grassy edge of pond $\frac{3}{4}$ mile east of Five Mile Point, Keweenaw County, *F. J. Hermann* 8081 (July 16, 1936) (H, M).

Newf. to Mich. and Wisc., southw. to Md.; also on the Pacific coast in Wash. and Vancouver Isl.

Section 13. DEWEYANAE

Perigynia 1-1.3 mm. broad, strongly nerved; scales oblong; leaves 1-2.5 mm. wide.

.....39. *C. bromoides*

Perigynia 1.6-1.9 mm. broad, nerveless or faintly nerved; scales ovate; leaves

2-5 mm. wide40. *C. Deweyana*

39. CAREX BROMOIDES Schkuhr

Common in the southern half of the Lower Peninsula in marshy woods and thickets, in swamps, on borders of ponds and on boggy banks of streams in woods; infrequent in wet meadows. Only one collection has been seen from Gogebic County, *E. A. Bessey & H. T. Darlington* 3127 (June 8, 1920) (S). north of the Grand River Valley: near power house, mouth of Montreal River,

Que. to Wisc., southw. to Fla. and La.

40. CAREX DEWEYANA Schwein.

Apparently absent from the southeasternmost counties, otherwise frequent to common throughout the state in woods and thickets. In its choice of habitats it seems to be indifferent to moisture content, being found with equal frequency on dry sandy ridges in aspen woods and moist beech-maple ravines or even wet thickets, swamps and arbor vitae bogs.

Labr. and Newf. to B. C., southw. to Pa., Iowa and Colo.

Section 14. OVALES

Bracts not leaf-like, not conspicuously exceeding the head.

Scales shorter than the perigynia and noticeably narrower above, largely exposing the perigynia above.

Wing of perigynium not narrowed near the middle of the body; leaf-blades of sterile culms erect or ascending, usually clustered toward the top; sterile culms often poorly developed.

Perigynia not obovate, widest near the middle or base.

Leaf-sheaths strongly white-hyaline ventrally.

Perigynia lanceolate-subulate to narrowly ovate-lanceolate, 3 to 4 times as long as wide.

Perigynia lanceolate-subulate, 0.8-1.2 mm. wide, 4 mm. long, the margin nearly obsolete at the base41. *C. Crawfordii*

Perigynia lanceolate to narrowly ovate-lanceolate, 1.2-2 mm. wide, 4-6.5 mm. long, noticeably wing-margined to the base.....42. *C. scoparia*

Perigynia ovate-lanceolate or broader, at most twice as long as wide.

Perigynia narrowly to broadly ovate, 3-4 mm. long.

Leaf-blades 1.5-4.5 (averaging 2.5) mm. wide; sheaths not mottled with green and white dorsally.

Perigynia 3-3.5 mm. long; spikes closely aggregated, not clavate

at the base43. *C. Bebbii*

Perigynia 3.5-4.5 mm. long; spikes not aggregated, usually in a flexuous, moniliform inflorescence, clavate at the base

.....44. *C. tenera*

Leaf-blades 2.5-6 (averaging 4) mm. wide; sheaths mottled with green and white dorsally; perigynia less abruptly beaked and the beak narrower than in *C. tenera*.....45. *C. normalis*

Perigynia (2.75) 3.5-6.5 mm. long, the body suborbicular.

Perigynia coriaceous or subcoriaceous, usually plano-convex, thick, 3.5-5.5 mm. long.

Perigynia (2.75) averaging 3.5 (4) mm. long, the beak half the length of the body or more; achenes 1.5 mm. long, oblong-ovoid; spikes in a moniliform inflorescence46. *C. festucacea*

Perigynia 3.75-5.5 mm. long, the beak less than half the length of the body; achenes 1.75-2 mm. long, orbicular or sub-orbicular when fully mature; spikes aggregated or in a moniliform inflorescence.

Achenes suborbicular, 1.25 mm. wide; perigynia ovate, sub-membranaceous, few-nerved ventrally, broadest near the base, tapering into the beak, the beak broader than in *C. brevior*, especially toward the base.....47. *C. molesta*

Achenes orbicular at maturity, 1.5-1.75 mm. wide; perigynia broadly ovate to suborbicular, coriaceous, usually nerveless or nearly so ventrally, broadest near the middle, abruptly contracted into the beak.....48. *C. brevior*

Perigynia membranaceous, flat and thin, 4-6.5 mm. long.

Perigynia nerveless ventrally or faintly few-nerved at the base,

- not translucent, 4-5 mm. long.....49. *C. Merritt-Fernaldii*
 Perigynia finely but strongly about 10-nerved ventrally, nearly translucent, 5.5-6.5 mm. long50. *C. Bicknellii*
 Leaf-sheaths green and strongly nerved ventrally nearly to the mouth.
 Scales cuspidate or even obtuse; perigynia nerveless or nearly so ventrally; spikes 2-5, aggregated into a stiff head....51. *C. suberecta*
 Scales long-acuminate to aristate; perigynia nerved ventrally; spikes 4-8, in a very flexuous inflorescence.....52. *C. Richii*
 Perigynia obovate, the body widest near the top.
 Scales obtuse to short-acuminate; achenes sessile or substipitate; perigynia 1.5-3 mm. wide.
 Tips of perigynia appressed; perigynia with body rounded at the apex; spikes approximate or aggregated, greenish to silvery brown.
 Perigynia nerveless ventrally; spikes 5-25, densely aggregated; leaf-blades of sterile culms 3.5-5 mm. wide.....53. *C. cumulata*
 Perigynia nerved ventrally; spikes 3-10, aggregated or somewhat separate; leaf-blades of sterile culms 2.5-3 mm. wide; scales either nearly equaling the perigynia or blunt.....54. *C. Longii*
 Tips of perigynia spreading; perigynia with body truncate-rounded at the apex, very abruptly beaked; spikes not aggregated, not silvery; scales acute, conspicuously shorter than the perigynia.....55. *C. abolutescens*
 Scales long-acuminate to aristate; achenes slenderly stipitate; perigynia 2.5-4 mm. wide56. *C. alata*
 Wing of perigynium rather abruptly narrowed near the middle of the body; leaf-blades of sterile culms widely spreading, numerous, not clustered at the apex; sterile culms strongly developed.
 Achenes oblong-oval, 1.5 mm. long; perigynia 3-7 mm. long; spikes 4-15 mm. long; ligule much wider than long.
 Perigynia scarcely distended over the achenes, thin and scale-like.
 Tips of perigynia appressed or ascending; spikes suborbicular-turbinate to obovoid-turbinate, 5-12 mm. long; leaf-blade firm; culms stiff57. *C. tribuloides*
 Tips of perigynia loosely ascending or somewhat recurved; spikes suborbicular, not turbinate, 4-8 mm. long; leaf-blades flaccid; culms not stiff58. *C. projecta*
 Perigynia obviously distended over the achenes, plano-convex, the tips widely spreading to strongly recurved; culms stiff; head dense, oblong59. *C. cristatella*
 Achenes linear-oblong, 2.5 mm. long; perigynia 7-10 mm. long; spikes 16-25 mm. long; ligule as wide as long.....60. *C. muskingumensis*
 Scales about the length of the perigynia and nearly the same width above, nearly concealing the perigynia above.
 Inflorescence stiff, the spikes aggregated or approximate.....61. *C. adusta*
 Inflorescence flexuous or moniliform, not stiff, at least the lower spikes remote.
 Perigynia dull-green, usually black dorsally at maturity, plump, nerveless ventrally or only faintly short-nerved; scales dull- or yellowish-brown.....62. *C. aenea*
 Perigynia greenish-white, strongly nerved ventrally; scales silvery-green.....63. *C. foenea*
 Bracts leaf-like, many times exceeding the head64. *C. sychnocephala*

41. CAREX CRAWFORDII Fern.

Common in sandy open ground, either dry or moist, especially on shores of lakes, and in swamps and bogs, in the Upper Peninsula. Rare in the Lower

Peninsula and there known from only Emmet and Cheboygan Counties.

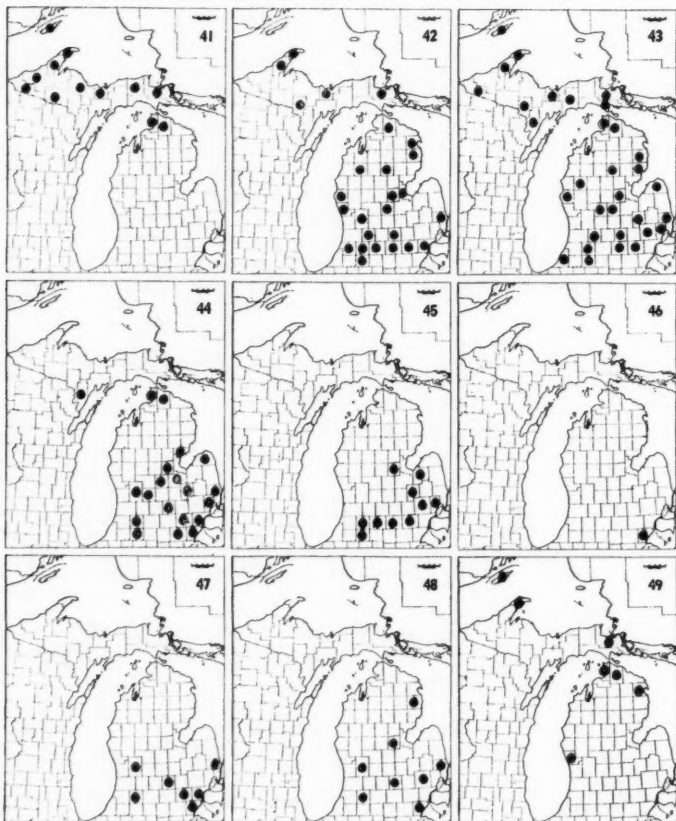
Newf. to B. C., southw. to Conn., N. J., Mich. and Wash.

42. *CAREX SCOPARIA* Schkuhr

C. scoparia var. *condensa* Fern.; *C. scoparia* f. *condensa* (Fern.) Kükenth.

Common in swamps, wet meadows and on borders of lakes; frequently forming extensive colonies. The form with spikes spreading and crowded in a dense head (f. *condensa* (Fern.) Kükenth.) is frequent throughout the state, but is not often well-marked.

Newf. to B. C., southw. to D. C., N. Mex. and Oreg.



41. *C. Crawfordii* Fern.; 42. *C. scoparia* Schkuhr; 43. *C. Bebbii* Olney; 44. *C. tenera* Dewey; 45. *C. normalis* Mack.; 46. *C. festucacea* Schkuhr; 47. *C. molestula* Mack.; 48. *C. brevior* (Dewey) Mack.; 49. *C. Merrill-Fernaldii* Mack.

43. CAREX BEBBII Olney

C. tribuloides var. *Bebbii* (Olney) Bailey

Common on wet, sandy beaches, in open bogs, marshes and swampy thickets; infrequent in moist woods.

Although the narrower leaf-blades of this species (2 to 4.5 mm. wide) and its relatively longer, generally acuminate to acute pistillate scales generally set it off from *C. cristatella* with leaf-blades 3-7 mm. wide and shorter scales with dilated, hyaline, blunt tips, occasional plants are found which apparently are intermediate in all characters. Examples of such transitional forms are: J. H. & L. S. Ehlers, July 11, 1923, grassy clearings in Thuja bog, Burt Lake, Cheboygan County; and, H. A. Gleason, July 27, 1935, moist, sedgy swale, Cheboygan County. Although such plants are not sterile, which is the expected condition in *Carex* hybrids, the suggestion of hybridity is marked, and Mackenzie has designated several such collections as crosses between the two species.

Newf. to B. C., southw. to N. J., Ill., Colo. and Wash.

44. CAREX TENERA Dewey

C. straminea var. *echinodes* Fern.; *C. straminea* of recent authors, not Willd.

Fairly common in the southern counties, becoming infrequent northward and rare north of Saginaw Bay. It is found in open woods, fields and thickets and less commonly in swamps and marshes.

Que. to Alberta, southw. to D. C., N. C. and Ill.

45. CAREX NORMALIS Mack.

C. mirabilis Dewey; *C. straminea* var. *mirabilis* (Dewey) Tuckerm.

Frequent in rich or alluvial woods and low thickets and infrequent in dry open habitats in the southern half of the Lower Peninsula.

Maine to Man., southw. to N. C. and Okla.

46. CAREX FESTUCACEA Schkuhr

A southern species known in Michigan from a single collection: Temperance, Monroe County, O. A. Farwell 8004 (July 13, 1927) (M). Its preferred habitats are low oak woods and moist roadside ditches. *Carex festucea* of Beal's "Flora," reported as "common throughout," is doubtless referable to a composite of *C. brevior*, *C. molesta* and *C. Merritt-Fernaldii* rather than to Schkuhr's species.

Mass. to Ind. and Iowa, southw. to Ga. and La.

47. CAREX MOLESTA Mack.

Frequent in the four southernmost tiers of counties, along streams and in moist openings in woods and in clayey meadows.

N.Y. to Kans. and Nebr.

48. CAREX BREVIOR (Dewey) Mack.

C. festucea var. *brevior* (Dewey) Fern.

Infrequent in the southern counties; rare north of Saginaw Bay. Found in dry, open habitats and less frequently in woods and along moist ditches.

Que. to B. C., southw. to D. C., Tenn., Tex., N. Mex. and Oreg.

49. CAREX MERRITT-FERNALDII Mack.

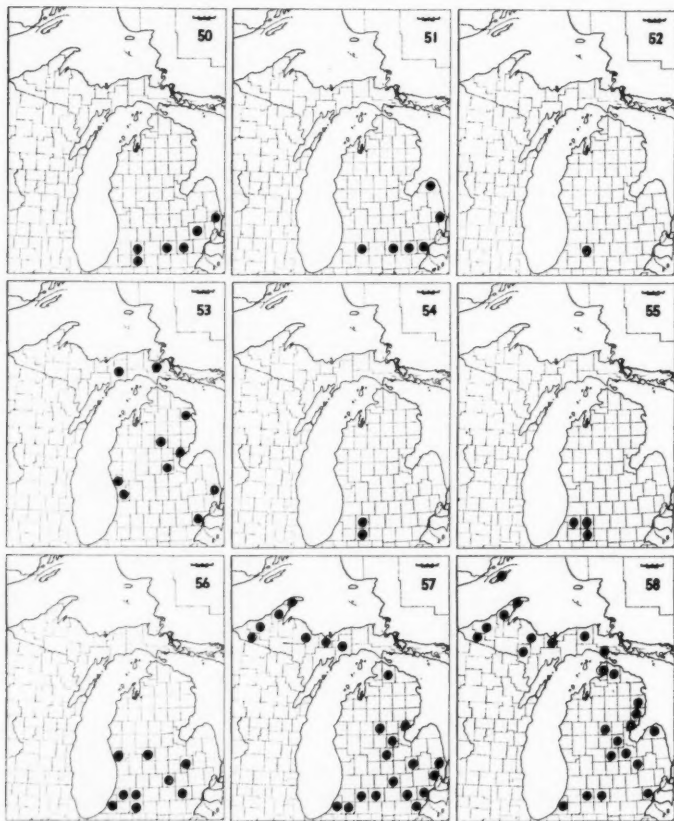
Infrequent in northern Michigan in open or partially open, sandy habitats

and in crevices in rock, generally not far from the shores of the Great Lakes. An outlying southern station is known in Muskegon County: Big Rapids Junction, *C. D. McLouth* (July 8, 1899) (S).

Maine to Man., southw. to Mass. and N. Y.

50. *CAREX BICKNELLII* Britt.

Frequent but local in the four southernmost tiers of counties. It is found in dry open ground, especially along roadsides, and rarely in low sandy habitats. Maine to Sask., southw. to Del., Ark. and Okla.



50. *C. Bicknellii* Britton; 51. *C. suberecta* (Olney) Britton; 52. *C. Richii* (Fern.) Mack.; 53. *C. cumulata* (Bailey) Mack.; 54. *C. Longii* Mack.; 55. *C. albolutescens* Schwein.; 56. *C. alata* Torr.; 57. *C. tribuloides* Wahl.; 58. *C. projecta* Mack.

51. CAREX SUBERECTA (Olney) Britt.

C. straminea var. *ferruginea* (Gray) Bailey

Locally frequent in marshes and open swamps in the southern two tiers of counties, becoming rare northward to Saginaw Bay.

Ont. to Minn., southw. to Va. and Mo.

52. CAREX RICHII (Fern.) Mack.

C. hormathodes var. *Richii* Fern.

Known in Michigan from a single station only: marsh 2 miles northwest of Vicksburg, Kalamazoo County, *C. R. & F. N. Hanes* (June 19, 1937) (H, Hn) and *F. J. Hermann* 9004 (July 9, 1937) (G, M, NY). It generally forms large stools in marshes, open swampy woods and on borders of woodland ponds.

Mass. to Mich. and Ind., southw. to N. J. and D. C.

53. CAREX CUMULATA (Bailey) Mack.

C. albolutescens var. *cumulata* Bailey

A local species occurring in Michigan at widely scattered stations in open sandy, usually moist, habitats. The majority of the known localities for it are in the vicinity of the Great Lakes.

N. S. to N. J., westw. to Sask.

54. CAREX LONGII Mack.

C. albolutescens of recent authors, not Schwein.

Known in Michigan only from Kalamazoo and St. Joseph Counties. Mr. C. R. Hanes has collected it at five stations in Kalamazoo County and Mr. F. W. Rapp at two. It is found in low, peaty maple woods, on grassy borders of swamps and wet shores of lakes.

Mass. to S. A.; n.w. Ind. and sw. Mich.; also in Bermuda.

55. CAREX ALBOLUTESCENS Schwein. (*Rhodora* 40:329. 1938.)

C. straminea of Mack., probably not of Willd.

Three collections of this species have been seen from the state: South Haven, Van Buren County, *C. H. Kauffman* (July 25, 1910) (M); border of swamp 2 miles south of Portage, Kalamazoo County, *C. R. & F. N. Hanes* 1224 (July 3, 1934) (Hn); and, marshy woods, Portage Lake, St. Joseph County, *C. R. & F. N. Hanes* 395 (June 18, 1939) (M).

N. S. southw. along the coast to Fla., westw. along the Gulf to Tex. and northw. in the Mississippi Valley to Ind. and sw. Mich.

56. CAREX ALATA Torr.

Frequent south of the Muskegon River. It occurs in swamps and on marshy borders of lakes but as a rule only a few plants are found at a station.

Mass. to Fla. and Tex., westw. to Mich., Ind. and Mo.

57. CAREX TRIBULOIDES Wahl.

C. tribuloides var. *turbata* Bailey; *C. tribuloides* var. *sangamonensis* Clokey.

Common in swamps, marshes, low woods and thickets, swales and wet ditches.

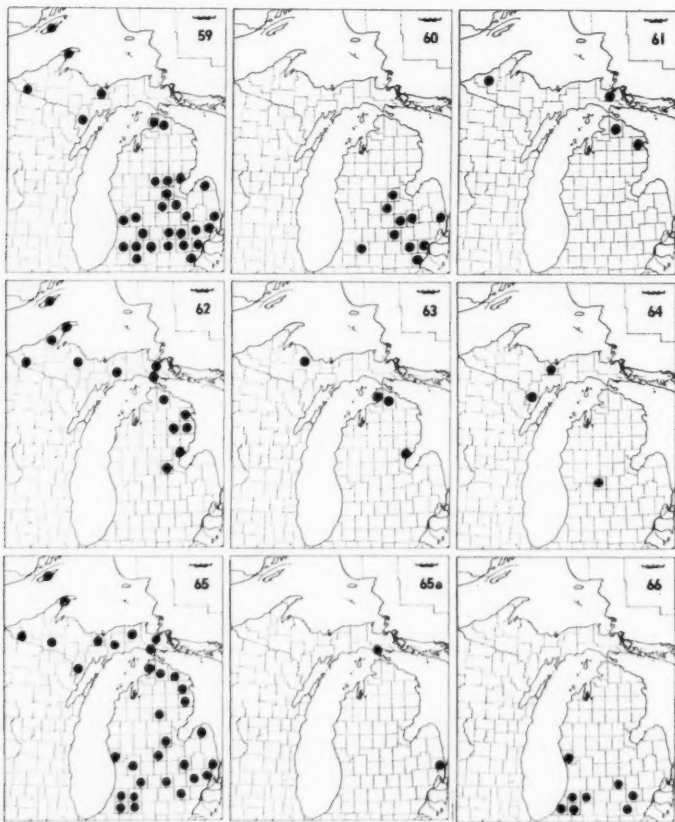
Que. to Minn., southw. to Fla. and La.

58. *CAREX PROJECTA* Mack.

C. tribuloides var. *reducta* Bailey; *C. tribuloides* var. *moniliformis* (Tuckerm.) Britt.

Common, especially northward, in habitats similar to those of the preceding species except that it is partial to shadier and somewhat drier situations. Rare in the southern three tiers of counties.

Newf. to B. C., southw. to N. J., Pa. and Iowa.



59. *C. cristatella* Britton; 60. *C. muskingumensis* Schwein.; 61. *C. adusta* Boott;
62. *C. aenea* Fern.; 63. *C. foenea* Willd.; 64. *C. sychnocephala* Carey; 65. *C. leptalea*
Wahl.; 65a. *C. leptalea* var. *Harperi* (Fern.) Stone; 66. *C. Jamesii* Schwein.

59. CAREX CRISTATELLA Britt.

C. cristata Schwein., not Clairv.

Very common from Saginaw Bay southward, becoming infrequent northward. It is found in wet habitats of all types except in deep woods and in very sandy soils.

Mass. to N. Dak., southw. to Va. and Mo.

60. CAREX MUSKINGUMENSIS Schwein.

Infrequent from Midland County southward; chiefly in the southeastern counties. It is partial to rich soils in low, alluvial woods and swampy thickets.

Ohio and Ky. to Man., Kans. and Ark.

61. CAREX ADUSTA Boott

Very local in northern Michigan. Four collections are known from the state: low ground 6 miles west of Alpena, Alpena County, *C. F. Wheeler* (July 11, 1895) (M, S); burnt-over aspen woods back of Bryant's, Cheboygan County, *L. E. Smith* 40 (July 10, 1917) (M); dry, open ground on right bank of Tahquamenon River above Emerson, Chippewa County, *C. K. Dodge* (August 28, 1914) (M); and, dry soil, summit of Porcupine Mountains, Ontonagon County, *H. T. Darlington & E. A. Bessey* 1028 (August 4, 1923) (H, S). Specimens to confirm the reports for Crawford County by Beal could not be found.

Newf. to Maine and N. Y., westw. to Minn., Sask. and Mackenzie.

62. CAREX AENEAE Fern.

C. foenea of Michigan authors, not Willd.

Infrequent in the eastern counties north of the Saginaw River, becoming frequent to common in the Upper Peninsula, in open sandy or rocky habitats.

Labr. to Conn., westw. to B. C. and Yukon.

63. CAREX FOENEA Willd.

C. foenea var. *perplexa* Bailey; *C. argyrantha* Tuckerm.

Most of the Michigan reports for this species are referable to *C. aenea*. Authentic collections have been seen from only four counties in the state: near Omer, Arenac County, *C. F. Wheeler* 356 (August 13, 1900) (S); in aspens north of Pellston, Emmet County, *L. E. Smith* 297 (July 17, 1920) (M); aspen association, Douglas Lake, Cheboygan County, *J. H. & L. S. Ehlers* 2362 (June 28, 1923) (M); and, sandy roadside 1 mile east of Champion, Marquette County, *F. J. Hermann* 7716 (June 27, 1936) (NY).

N. S. and Que. to Mich., southw. to Va. and Ohio.

64. CAREX SYCHNOCEPHALA Carey

An extremely local species, known in Michigan from only three collections: Montcalm County, *C. F. Wheeler* (September, 1875) (S); bottom land and river banks on Experiment Station grounds, near Chatham, Alger County, *C. F. Wheeler* 175 (August 22, 1900) (M, S); and, edge of river, Sugar Beet Island, Menominee, Menominee County, *C. O. Grassl* 2565 (July 25, 1933) (H, M).

Ont., N. Y. and Iowa, westw. to Sask., Mont. and Wash.

Section 15. POLYTRICHOIDEAE

- Perigynia 2.5-3.5 mm. long, slightly overlapping; achenes lustrous, obtusely angled.65. *C. leptalea*
 Perigynia 4-5 mm. long, strongly overlapping; achenes barely lustrous, sharply angled65a. *C. leptalea* var. *Harperi*

65. CAREX LEPTALEA Wahl.

Very common throughout, in sphagnum in tamarack, black spruce, Chamaedaphne and Thuja bogs, and occasional in swampy woods, marshes and wet peaty meadows.

Newf. to B. C., southw. to Pa., Mo., Colo. and Calif.

65a. CAREX LEPTALEA var. HARPERI (Fern.) Stone
C. Harperi Fern.

This southeastern variety is represented by two collections of characteristic material from Michigan: bogs and very wet places, St. Clair County, C. K. Dodge 1023 (May 27, 1894) (M, S); and, open bogs, Bois Blanc Island, Mackinac County, C. K. Dodge (June 18, 1914) (M). The known distribution of this sedge in the state corresponds to that of such other Coastal Plain species as *Juncus militaris*, *Panicum meridionale* var. *albemarlense*, *Bartonia virginica*, *Solidago graminifolia* var. *Nuttallii*, *Drosera intermedia*, *Muhlenbergia uniflora* and *Juncus pelocarpus* and suggests that it may have entered the Great Lakes area by a similar migratory route from the east.

N. J. to Fla., westw. to Mich., Ind. and Tex.

Section 16. PHYLLOSTACHYAE

- Pistillate scales not enveloping the perigynia, not leaflike, green with hyaline margins; leaf-blades 2-3 mm. wide66. *C. Jamesii*
 Pistillate scales concealing and partly enveloping the perigynia, leaf-like, without hyaline margins; leaf-blades 2.5-6 mm. wide67. *C. Backii*

66. CAREX JAMESII Schwein.

Rare in Muskegon County and infrequent in the three southernmost tiers of counties, in rich woods. Its preferred habitat is rich wooded ravines. The report in Beal's "Flora" for Keweenaw County should doubtless be referred to *C. Backii*.

Ont. and N. Y. to Iowa, southw. to W. Va., Mo. and Kans.

67. CAREX BACKII Boott
C. durifolia Bailey

In dry rocky and sandy soils either in the open or in open woods, from Alcona County northward. Rare to locally infrequent.

Que. to Mass. and N. Y., westw. to Alberta and B. C.

Section 17. MONTANAE

- Fertile culms all alike, elongated (7-40 cm. long), bearing both staminate and pistillate spikes; basal spikes absent.
 Body of perigynium elliptic to oblong-ovoid, much longer than wide; staminate spike slender.
 Scales about half the length of the mature perigynium-bodies, suborbicular, obtuse to short-mucronate; perigynia 3.5 mm. long, hirsute68. *C. Peckii*

Scales exceeding the mature perigynium-bodies, ovate, acuminate or cuspidate; perigynia 2.75-3.5 mm. long, puberulent.

Staminate scales closely appressed, obtuse or short-acute, not cucullate at the tip, the midvein usually not extending to the tip; pistillate spikes usually not aggregated; culms erect. 69. *C. aritlecta*

Staminate scales ascending to loosely spreading, the midrib extending to the tip; at least the upper pistillate spikes closely aggregated or congested; culms weak, generally more or less arcuate. 70. *C. Emmonsii*

Body of perigynium suborbicular to somewhat obovoid, about as long as wide. Ligule conspicuous, longer than wide; lowest bract truncate or bifid and abruptly awned or, in var. *Wheeleri*, leaf-like; leaf-blades 2.5-4.5 mm. wide; culms little fibrillose at the base, without long, horizontal stolons.

Staminate spike conspicuous, 10-20 mm. long, peduncled; lowest bract not leaf-like, generally less than 2 cm. long; leaves usually more than half the height of the culms. 71. *C. communis*

Staminate spike inconspicuous, generally 4-6 mm. long, sessile or sub-sessile; lowest bract leaf-like, often 3-5 cm. long; leaves numerous, broad, usually less than half the height of the culms. 71a. *C. communis* var. *Wheeleri*

Ligule short, much wider than long; lowest bract usually gradually acuminate; leaf-blades 2.5 (very rarely 3) mm. wide or less; culms conspicuously fibrillose at the base, with long horizontal stolons; staminate spike stout.

Beak of perigynium less than half the length of the body; achene obovoid. Terminal spike staminate. 72. *C. pennsylvanica*

Terminal spike largely pistillate, bearing a few scattered staminate flowers. 72a. *C. pennsylvanica* f. *androgyna*

Beak of perigynium about as long as the body; achene obovoid-orbicular. 73. *C. lucorum*

Fertile culms of two types, some short (1-5 cm. long), partly hidden among the densely tufted leaf-bases and bearing only pistillate spikes, others elongated (5-11 cm. long) and bearing staminate spikes only or both staminate and pistillate spikes.

Bract of the lowest non-basal pistillate spike leaf-like, normally exceeding the culm; culms little, if at all, fibrillose at the base.

Perigynia 2.5 mm. long, short-beaked (0.5 mm. long); staminate spike inconspicuous, 2-5 mm. long, 0.5-1 mm. wide; rootstocks slender. 74. *C. deflexa*

Perigynia 3-4.5 mm. long, the beak 0.75-1.5 mm. long; staminate spike conspicuous, 3-15 mm. long, 1-2.5 mm. wide; rootstocks stout. 75. *C. Rossii*

Bract of the lowest non-basal pistillate spike scale-like, shorter than the culm; culms strongly fibrillose at the base.

Leaf-blades rather thin, not stiff, erect or ascending, 1.5-3 mm. wide; perigynia membranaceous, 2.25-4 mm. long, the body short-pubescent above.

Perigynia 2.25-3.25 mm. long, 1-1.25 mm. wide, the beak about half the length of the body; achenes orbicular-obovoid. 76. *C. umbellata*

Perigynia 3.25-4 mm. long, 1.25-1.5 mm. wide, the beak nearly the length of the body; achenes oblong-obovoid, minutely roughened. 77. *C. rugosperma*

Leaf-blades thick, rigid, widely spreading at maturity, 2-4.5 mm. wide; perigynia subcoriaceous, 3.5-4.5 mm. long, the body glabrous or very sparsely pubescent above. 78. *C. lousa*

68. CAREX PECKII Howe

C. albicans of authors, not Willd.

Infrequent north of the Saginaw River Valley in open woods and thickets, usually in rocky or sandy soils.

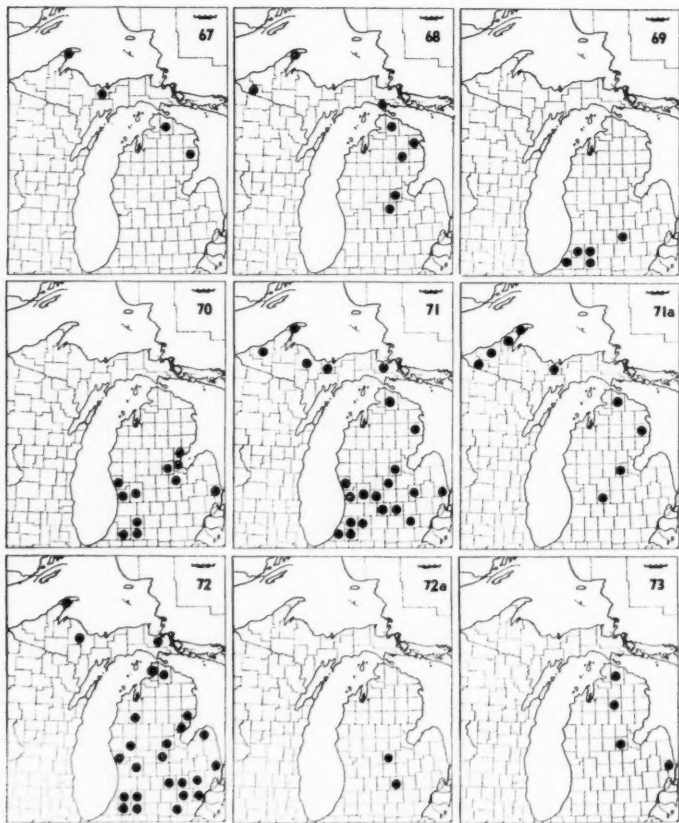
Que. and Yukon southw. to N. J., Mich., S. Dak., Sask. and B. C.

69. CAREX ARTITECTA Mack.

C. varia Muhl., not Lumnitzer nor Host.

Rare in the southern three tiers of counties, chiefly in the southwestern corner of the state. It occurs in dry open woods and sandy clearings. The report (as *C. varia*) for Gogebic County by Darlington (Papers Mich. Acad. Sci. 1:76. 1923) should be referred to *C. Peckii*; doubtless, Beal's report for Keweenaw County is likewise referable to the latter species.

Vt. to Iowa, southw. to Ga. and Okla.



67. *C. Bachii* Boott; 68. *C. Peckii* Howe; 69. *C. artitecta* Mack.; 70. *C. Emmonsii* Dewey; 71. *C. communis* Bailey; 71a. *C. communis* var. *Wheeleri* Bailey; 72. *C. pennsylvanica* Lam.; 72a. *C. pennsylvanica* f. *androgyna* Hermann; 73. *C. lucorum* Willd.

70. CAREX EMMONSII Dewey

C. albicans of authors, doubtfully of Willd.

Infrequent to frequent in the southern counties northward to Saginaw Bay, in open sandy woods, on moist sandy borders of marshes or thickets and on plains.

N. S. to Fla. and about the Great Lakes.

71. CAREX COMMUNIS Bailey

C. pedicellata (Dewey) Britt.

Common, except in sandy soils, in southern Michigan, becoming infrequent northward. It is found in dry woods, especially in cut-over and second-growth woods, and occasionally in clearings.

N. S. to Minn., southw. to Ga., Ky. and Ark.

71a. CAREX COMMUNIS var. WHEELERI Bailey

C. pedicellata var. *Wheeleri* (Bailey) Britt.

Infrequent in central Michigan and frequent on the Keweenaw Peninsula in woods, on shores of lakes and banks of rivers; generally in moister habitats than the species. In its extremes this is a well marked variety. Bailey, in his original description, points out that in aspect it resembles *C. artitecta* except for the broad leaves and large perigynia, and the plant is usually much coarser in habit.

N. S. to Conn. and Mich.

72. CAREX PENNSYLVANICA Lam.

Very common in southern Michigan becoming less frequent northward, in open woods and dry, sandy or rocky, open ground. It prefers somewhat more open habitats and more sterile soils than *C. communis*. In the southern counties it is often abundant on open oak slopes.

N. S. to N. Dak., southw. to S. C., Tenn. and Iowa.

72. CAREX PENNSYLVANICA f. ANDROGYNA Wheeler ex Hermann*

A form in which the normally staminate terminal spike is almost wholly pistillate, bearing only a few scattered staminate flowers. Wheeler had designated the type sheet as 'forma androgyna, f. nov.' but apparently did not publish the name. Three collections are known: near Alma, Gratiot County, C. A. Davis (June 29, 1883) (H, M); and, dry clay hillside near Michigan State College, East Lansing, Ingham County, C. F. Wheeler (May 20, 1893) (M) and (May 25, 1893) (M (TYPE)).

73. CAREX LUCORUM Willd.

C. pennsylvanica var. *lucorum* (Willd.) Fern.

Rare; chiefly in dry open woodlands. Collections from four counties have been seen: woods, Port Huron, St. Clair County, E. C. Almendinger (June 8, 1883) (M); hillside thicket 2 miles west of Greendale, Midland County, R. R. Dreisbach 5763 (June 9 1928) (D); tamarack swamp, 10 miles east of

* *Carex pennsylvanica* Lam. f. *androgyna* f. nov. A forma typica recedit spica terminali maxima ex parte feminea.

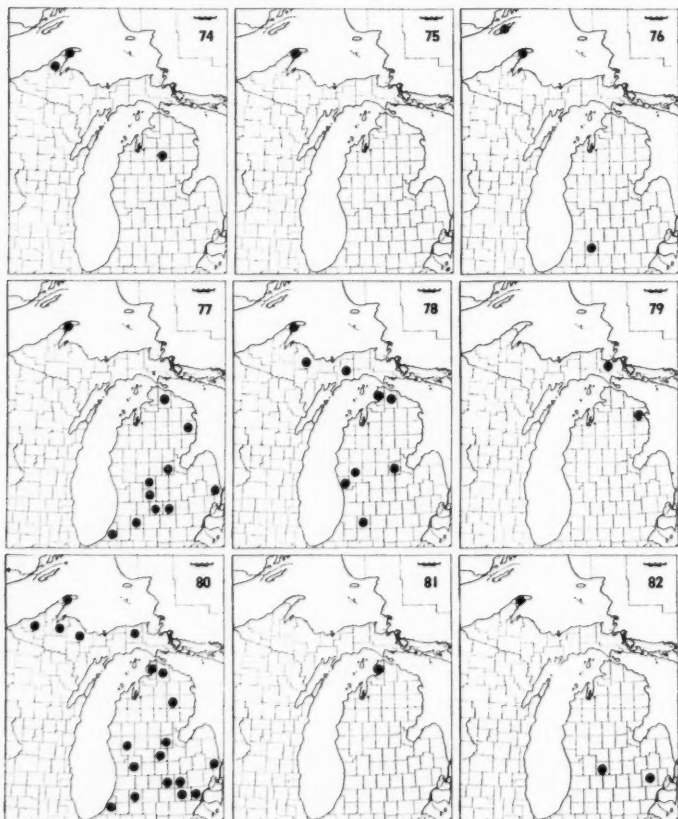
Grayling, Crawford County, without collector (June 16, 1888) (S); and, sandy soil, aspen association, Douglas Lake region, Cheboygan County (?), L. E. Smith 24 (July 9, 1917) (M).

N. S. to Wisc., southw. in the mountains to N. C.

74. *CAREX DEFLEXA* Hornem.

C. deflexa var. *Deanei* Bailey

A boreal species known in Michigan from five collections: low ground near Grayling, C. F. Wheeler (May 14, 1898) (M, S); humus bordering trail in



74. *C. deflexa* Hornem.; 75. *C. Rossii* Boott; 76. *C. umbellata* Schkuhr; 77. *C. rugosperma* Mack.; 78. *C. tonsa* (Fern.) Bickn.; 79. *C. scirpoidea* Michx.; 80. *C. pedunculata* Muhl.; 81. *C. concinna* R.Br.; 82. *C. Richardsonii* R.Br.

mixed forest near shore of Keweenaw Bay, southwest of Jacobsville, Houghton County, *F. J. Hermann* 7630 (June 23, 1936) (G, H, M, NY); sandy hills sparsely covered with shrubs etc. near Clifton, Keweenaw County, *O. A. Farwell* 734 (July 7, 1890) (M, S); low fields and swales, Keweenaw County, *O. A. Farwell* 745 (July 12, 1890) (M); and, forming carpets on knolls in arbor vitae swamp, Bête Gris, Keweenaw County, *M. L. Fernald & A. S. Pease* 3192 (July 5, 1934) (G, M, S).

Greenl. to Alaska, southw. to Mass., Mich. and B. C.

75. CAREX ROSSII Boott

C. deflexa var. *Farwellii* Britt.; *C. deflexa* var. *media* Bailey

A western sedge represented from the state only by the following collections from Keweenaw County: sandy parts of bluffs, *O. A. Farwell* 244 (June 1880) (S); windswept crests, crevices and talus of sandstone-conglomerate, West Bluff [3½ miles west of Copper Harbor], *M. L. Fernald & A. S. Pease* 3191 (July 4, 1934) (G, M) and *F. J. Hermann* 7519 (June 18, 1936) (H, M, NY, US); and, crevices in sandstone bluff on shore of Lake Superior, Esrey Park, Agate Harbor, *F. J. Hermann* 7616 (June 22, 1936) (H, NY).

Mountains of Colo. to Calif., northw. to Yukon, eastw. to the Black Hills of S. Dak. and locally to n. Mich.

76. CAREX UMBELLATA Schkuhr

C. umbellata var. *brevirostris* Boott; *C. abdita* Bickn.

Rare. The three known Michigan stations for it are: near Grand Trunk Railroad, 3½ miles east of Schoolcraft, Kalamazoo County, *C. R. & F. N. Hanes* 2897 (June 4, 1937) (Hn); Isle Royale, Keweenaw County, *P. E. Hebert* (June 10, 1933) (ND); and, crevices in sandstone bluff on shore near Silver Isle, Agate Harbor, Keweenaw County, *F. J. Hermann* 7619 (June 22, 1936) (H, M, NY, US). Its usual habitats, elsewhere in its range, are dry sandy soil in open woods and dry sterile fields. Most of the Michigan reports for this species should be referred to *C. rugosperma*.

Newf. to B. C., southw. to D. C. and Ill.

77. CAREX RUGOSPERMA Mack.

C. umbellata of recent authors, not Schkuhr; *C. umbellata* var. *vicina* of Beal in large part.

Frequent in sandy, open habitats, especially in dry clearings in aspen woods, in the Lower Peninsula. A single collection from the Upper Peninsula has been seen: bluffs near Clifton, Keweenaw County, *O. A. Farwell* 244 (June 28, 1885) (M).

N. S. to Minn., southw. to Md. and Ind.

78. CAREX TONSA (Fern.) Bickn.

C. umbellata var. *tonsa* Fern.

Infrequent in most of the Lower Peninsula becoming frequent northward and in the Upper Peninsula. It is partial to very sandy, usually dry and open, habitats such as dunes, sandy plains and shores.

Que. to Alberta, southw. to D. C. and Ind.

Section 18. SCIRPINAE

79. CAREX SCIRPOIDEA Michx.

A boreal sedge known from two localities in the state: rocky shore, Thunder Bay Island, Alpena County, *C. F. Wheeler* (July 18, 1895) (S); damp, open ground, Thunder Bay Island, Alpena County, *C. K. Dodge* 1088 (June 22, 1907) (M, S); and, Drummond Island, Chippewa County, without collector (August 3, 1839) (M). There is no specimen in either the herbarium of the University of Michigan or that of Michigan State College to corroborate Beal's report for Keweenaw County.

Greenl. to Alaska, southw. to N. H., Mich., Colo. and B. C.; also in arctic Eurasia.

Section 19. DIGITATAE

- Basal spikes present; terminal spike usually androgynous; pistillate scales abruptly cuspidate or short-awned80. *C. pedunculata*
 Basal spikes absent; terminal spike staminate; pistillate spikes blunt to acuminate.
 Staminate spike 3-6 mm. long; pistillate scales obtuse, ciliate, half the length of the perigynia81. *C. concinna*
 Staminate spike 8-25 mm. long; pistillate scales acute to acuminate, more than half the length of the perigynia82. *C. Richardsonii*

80. CAREX PEDUNCULATA Muhl.

Rare to infrequent in the two southernmost tiers of counties, probably absent from some of them; otherwise common throughout in rich woods, especially on beech-maple slopes.

Newf. to B. C., southw. to Ga., Iowa and S. Dak.

81. CAREX CONCINNA R. Br.

A single collection of this boreal species is known from Michigan: roadside through moist woods, Big Stone Bay [$3\frac{1}{2}$ miles west of Cecil Bay], Emmet County, *J. H. & L. S. Ehlers* 2697 (August 5, 1923) (M).

Newf. to Yukon, southw. to Que., n. Mich., S. Dak., Colo. and B. C.

82. CAREX RICHARDSONII R. Br.

Rare and very local. The following collections have been seen: Oakland County, *D. Cooley* (June 14, 1852) (S); associated with *C. siccata* and *C. pennsylvanica*, on sandy hillsides not far from the interurban station called Due West, near Rochester, Oakland County, *O. A. Farwell* 7910 (June 1, 1924) (H); bluffs along Fish Creek, Hubbardston, Ionia County, *C. F. Wheeler* 61 (June 1878) (M, S); bare, gravelly summit of West Bluff, $3\frac{1}{2}$ miles west of Copper Harbor, Keweenaw County, *M. L. Fernald & A. S. Pease* 2303 (July 4, 1934) (G) and, *F. J. Hermann* 7515 (June 18, 1936) (H, M, NY, S, US). Specimens to confirm Beal's reports for Gaylord and Orion and for Macomb County have not been located. In Indiana this species is restricted to moist sand dunes along Lake Michigan. It is a very evanescent plant, flowering and fruiting within a period of a few days (early in June in southern Michigan) and then rapidly withering away. In general aspect it resembles *C. pennsylvanica*.

Western N. Y. and Ont. to Alberta, southw. to Ill. and S. Dak.

Section 20. TRIQUETRAE

83. CAREX HIRTIFOLIA Mack.

C. pubescens Muhl., not Poir.

Common in moist, rich woods from Saginaw Bay southward.

N. B. to Minn., southw. to D. C., Ky. and Kans.

Section 21. ALBAE

84. CAREX EBURNEA Boott

C. setifolia (Dewey) Britt.

Frequent in calcareous soils. It is very commonly associated with arbor vitae, either on dry, rocky or sandy shores and limestone bluffs or in bogs. It occurs also in oak woods on marly and clay soils and frequently in damp, sandy habitats; rarely, too, in apparently acid habitats such as sandy depressions in jack pine plains.

Newf. to B. C., southw. to Ala., Mo. and Nebr.

Section 22. BICOLORES

Pistillate scales averaging three-fourths the length of the perigynia or more, reddish brown, appressed; terminal spike androgynous, rarely acuminate; mature perigynia white-pulverulent, elliptic-obovoid, not translucent or fleshy.....85. *C. Garberi*

Pistillate scales averaging one-half the length of the perigynia or less, generally pale yellowish brown and cuspidate, widely spreading at maturity; terminal spike staminate, rarely with a few perigynia at the base; perigynia golden yellow or brownish, orbicular-obovoid, translucent, fleshy.....86. *C. aurea*

85. CAREX GARBERI Fern. (Rhodora 37:253. 1935.)

C. bicolor of American authors, not All.; *C. Hassei* of recent authors, not Bailey.

Frequent along the shores of the Great Lakes from Saginaw Bay northward, and rare on the southeastern shore of Lake Michigan. Its preferred habitat is moist, sandy beaches but it is frequent also on limestone and on conglomerate shores; often associated with *C. viridula* and *C. Crawei*.

Que. to Mich., Ind., and Wisc.; also in Alberta and B. C.

86. CAREX AUREA Nutt.

Common in swamps and bogs, wet woods and thickets, and low peaty meadows; frequent on wet sandy shores. In open habitats the plants are commonly low, 2-4 inches high, erect and noticeably caespitose while in the deep shade they develop a markedly different habit, becoming lax and diffuse and often 20 inches or more high.

Newf. to B. C., southw. to Conn., Ind., Nebr., N. Mex. and Calif.

Section 23. PANICEAE

Perigynia beakless or with a very short beak.

Leaf-blades and perigynia strongly glaucous; leaf-blades 0.5-3.5 mm. wide, deeply channeled87. *C. livida* var. *Grayana*

Leaf-blades not glaucous, 2-7 mm. wide, flat above.

Culms phyllopodic; stolons deep-seated, slender, whitish; plants of open marly or sandy habitats.

Pistillate spikes linear to linear-oblong, 3.5-4.5 mm. wide; perigynia appressed or ascending, 2.5-3.5 mm. long, slightly excurved and tapering to the apex, very minutely beaked or beakless; leaf-blades 2-4 mm. wide; culms slender88. *C. tetanica*

Pistillate spikes oblong or linear-oblong, 5-8 mm. wide; perigynia spreading at maturity, 3-5 mm. long, abruptly narrowed at the apex into a minute, more or less strongly bent beak; leaf-blades 2.7-7 mm. wide; culms stout

89. *C. Meadii*

Culms strongly aphyllopodic; stolons superficial; plants of rich humus in shady woods

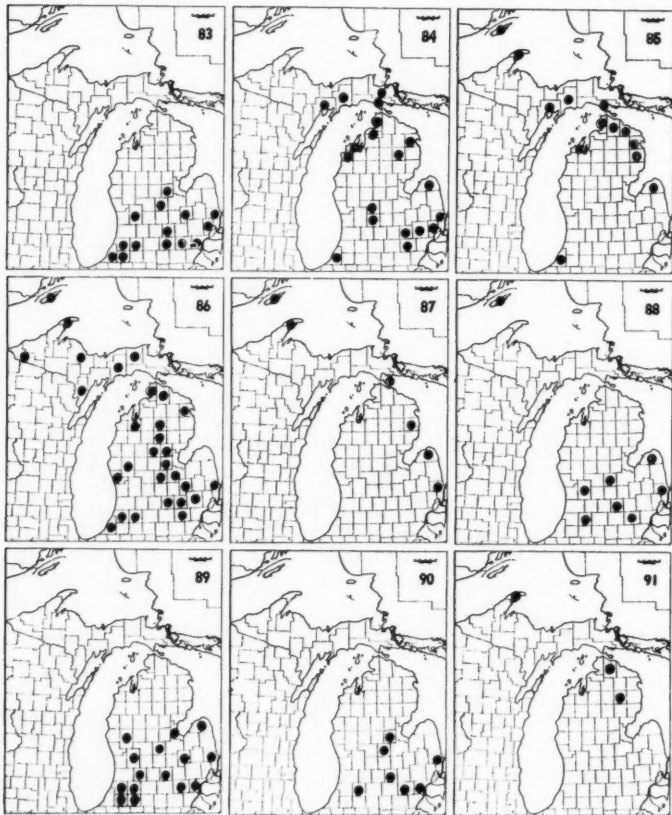
90. *C. Woodii*

Perigynia with a prominent slender beak one-fourth the length of the body.....

91. *C. saltuensis*

87. *CAREX LIVIDA* (Wahl.) Willd. var. *GRAYANA* (Dewey) Fern.

A rare sedge of sphagnum bogs and wet shores. It is known in Michigan



83. *C. hirtifolia* Mack.; 84. *C. eburnea* Boott; 85. *C. Garberi* Fern.; 86. *C. aurea* Nutt.; 87. *C. livida* var. *Grayana* (Dewey) Fern.; 88. *C. tetanica* Schkuhr; 89. *C. Meadii* Dewey; 90. *C. Woodii* Dewey; 91. *C. saltuensis* Bailey.

from five counties: near Port Huron, St. Clair County, *C. K. Dodge* (August 6, 1893) (S); plentiful in a very wet place west of Caseville, Huron County, *C. K. Dodge* (June 17, 1909) (M); low shoreline, Alcona County, *H. T. Darlington* 2144 (July 17, 1918) (S); abundant in open sphagnum bog, Bois Blanc Island, Mackinac County, *C. K. Dodge* (June 28, 1914) (M); infrequent in arbor vitae-black spruce bog southeast of Eagle Harbor, Keweenaw County, *F. J. Hermann* 8260 (July 4, 1936) (H, NY); and, in a quackberry bog near Scovill Point, Isle Royale, Keweenaw County, *C. A. Brown* 3083 (July 1, 1930) (M).

Labr. and Newf. to Alaska, southw. to N. J., n. N. Y., Mich. and Calif.

88. CAREX TETANICA Schkuhr

Infrequent from Saginaw Bay southward. Its habitats are swamps, wet meadows and prairies, and marshy borders of lakes, usually in marly or sandy soils. In the Upper Peninsula it is known only from Keweenaw County: wet places, Isle Royale, *J. H. Sandberg*, (June 1889) (S).

Mass. to Alberta, southw. to Pa. and Iowa.

89. CAREX MEADII Dewey

C. tetanica var. *Meadii* (Dewey) Bailey

Frequent to locally common northward to Saginaw Bay. It occurs in the habitats of *C. tetanica* but is also frequently found in dry open habitats, such as sandy roadside embankments and gravelly railroad sidings.

N. J. to Sask., southw. to Ga. and Tex.

90. CAREX WOODII Dewey

C. tetanica var. *Woodii* (Dewey) Bailey

Infrequent, but often occurring in colonies of considerable size in rich low woods, northward to Saginaw Bay. It seems to be somewhat periodic in its fruiting, the colonies sometimes remaining sterile and depauperate over a period of several years and then flourishing and fruiting abundantly during one or two seasons. This apparent periodicity may be correlated with the amount of annual precipitation.

N. Y. to Man., southw. to D. C. and Mo.

91. CAREX SALTUENSIS Bailey

C. vaginata of American authors; *C. altocaulis* (Dewey) Britt.

Rare in boggy thickets and woods in northern Michigan. The following four Michigan collections are the only ones which could be located: Comins, Oscoda County, without collector (June 14, 1888) (S); edge of roadway through Reese's Bog (a Thuja bog) near Douglas Lake, Cheboygan County, *L. E. Smith* 113 (July 27, 1917) (D, M); frequent in cedar swamps, Keweenaw County, *O. A. Farwell* 243 (July 1889) (H); and, rich humus on knolls bordering Thuja bog, 1¼ miles east of Eagle Harbor, Keweenaw County, *F. J. Hermann* 8130 (July 17, 1936) (H, M, NY).

Labr. and Newf. to Yukon, southw. to n. New England, n. N. Y., n. Mich., n. Minn. and B. C.

Section 24. LAXIFLORAE

- Bract-sheaths, base of culms, and staminate scales strongly red-tinged.
 Leaf-blades of fertile culms rudimentary, the sheaths concave at the mouth;
 bracts bladeless; perigynia 4-5 mm. long92. *C. plantaginea*
- Leaf-blades of fertile culms well-developed; the sheaths prolonged upward at
 the mouth; bracts with blades well-developed; perigynia 5.3-6 mm. long....
93. *C. Careyana*
- Bract-sheaths not red-tinged, base of culms rarely so; staminate scales greenish
 white to dull reddish brown-tinged.
 Perigynia sharply triangular, short tapering at the base, closely 35-50- nerved.
 Spikes erect, nearly sessile; leaf-blades very smooth except for the margins,
 the larger 12-25 mm. wide, those of the fertile culms much smaller than
 those of the sterile94. *C. platyphylla*
- Spikes drooping on filiform peduncles; leaf-blades hispidulous on the veins,
 2-12 mm. wide, those of the fertile culms moderately smaller than those
 of the sterile.
 Pistillate spikes without a staminate flower at the base; leaf-blades 2-5 mm.
 wide, erect, green95. *C. digitalis*
- Pistillate spikes with 1-2 staminate flowers at the base; leaf-blades 5-12 mm.
 wide, weak, glaucous green.
 Angles of the culms blunt, minutely serrulate only below the bracts;
 edges of the bract-sheaths entire; perigynia tapering at the apex,
 short-beaked96. *C. laxiculmis*
- Angles of the culms sharp, minutely serrulate; edges of the bract-sheaths
 minutely serrulate; perigynia rounded or round-tapering at the apex,
 blunt or abruptly short-beaked.....96a. *C. laxiculmis* var. *copulata*
- Perigynia obtusely triangular (at least below), long-tapering at the base.
 Bract-sheaths smooth on the edges or shallowly serrulate; beak of perigynium
 straight or slightly oblique.
 Culms, bract-sheaths and leaves coarsely granular; sterile shoots forming
 short culms; culms usually reddish at the base; beak of perigynium
 minute or very short97. *C. ormostachya*
- Culms, bract-sheaths and leaves not granular; sterile shoots reduced to tufts
 of leaves; beak of perigynium conspicuous98. *C. laxiflora*
- Bract-sheaths strongly serrulate on the edges.
 Perigynia nerveless or faintly nerved, membranaceous, elliptic-obovoid,
 rather sharply angled above, the beak straight or oblique; sterile shoots
 developing conspicuous culms99. *C. leptonervia*
- Perigynia conspicuously many-nerved, subcoriaceous, obovoid, very obtusely
 angled, the beak abruptly bent.
 Sterile shoots reduced to tufts of leaves, not forming culms; leaf-blades
 7-30 mm. wide; staminate spike very slender, inconspicuous; pistillate
 scales half the length of the perigynia or less, broadly obovate-
 orbicular, strongly divergent at the base100. *C. albusina*
- Sterile shoots developing conspicuous culms; leaf-blades 3-12 mm. wide;
 staminate spike conspicuous; pistillate scales mucronate to long-awned.
 Culms not reddish-tinged at the base; lower pistillate spikes not on
 long capillary peduncles; staminate scales usually greenish white or
 slightly tinged with reddish brown; staminate spike typically sessile
 or very short-peduncled; perigynia obovoid, 3-4 mm. long.
101. *C. blanda*
- Culms reddish-tinged at the base; lower pistillate spikes on long capil-
 lary peduncles; staminate scales strongly tinged with reddish
 brown; staminate spike long-peduncled; perigynia broadly obovoid,
 2.5-3.2 mm. long102. *C. gracilescens*

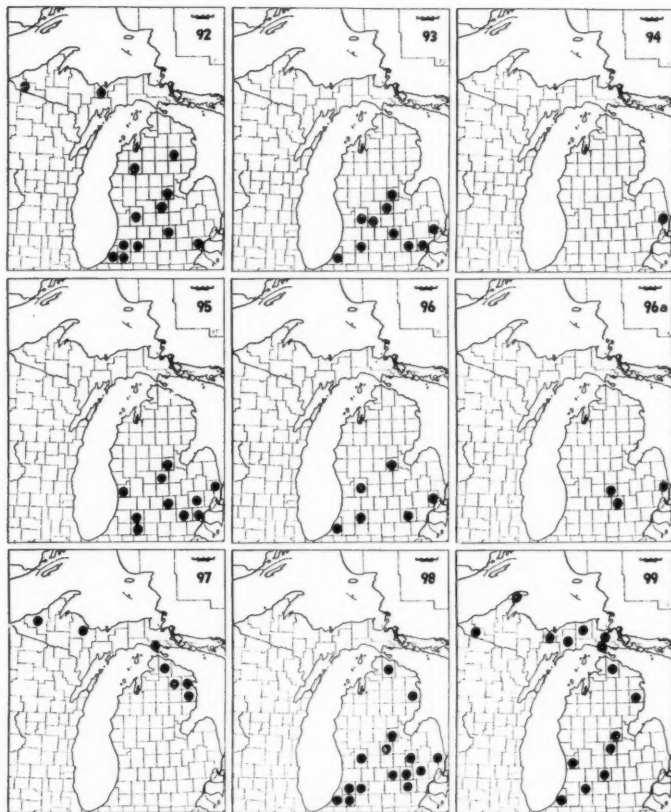
92. *CAREX PLANTAGINEA* Lam.

Frequent in the southern counties, becoming infrequent northward, in moist rich woods. Its preferred habitats are deep ravines and shady beech slopes.

Que. to Sask., southw. to N. C. and Ky.

93. *CAREX CAREYANA* Torr.

Locally frequent south of Saginaw Bay. It is found in moist rich hardwoods, particularly in ravines.



92. *C. plantaginea* Lam.; 93. *C. Careyana* Torr.; 94. *C. platyphylla* Carey;
95. *C. digitalis* Willd.; 96. *C. laxiculmis* Schwein.; 96a. *C. laxiculmis* var. *copulata*
(Bailey) Fern.; 97. *C. ormostachya* Wieg.; 98. *C. laxiflora* Lam.; 99. *C. leptoneuria*
Fern.

N. Y. to Mich., southw. to Va. and Mo.

94. *CAREX PLATYPHYLLA* Carey

Specimens to confirm the reports for this species from Grand Rapids, Hubbardston and St. Clair County in Beal's Flora could not be found. Only one Michigan collection was seen: wooded slope of Black River, 3 miles north-west of Veddo, St. Clair County, *F. J. Hermann* 7372 (May 16, 1936) (H, NY).

Que. to Mich., southw. to N. C. and Ill.

95. *CAREX DIGITALIS* Willd.

Frequent south of Saginaw Bay, in dry rocky or sandy woods.
Maine to Minn., southw. to Fla. and Tex.

96. *CAREX LAXICULMIS* Schwein.

Infrequent south of Saginaw Bay, in woods and thickets.
Maine to Wisc., southw. to N. C. and Mo.

96a. *CAREX LAXICULMIS* var. *COPULATA* (Bailey) Fern.

C. copulata (Bailey) Mack.; *C. digitalis* var. *copulata* Bailey.

Rare to infrequent in rich woods in southern Michigan.
N. J. to Mich. and Mo.

97. *CAREX ORMOSTACHYA* Wieg.

Infrequent north of Saginaw Bay in sandy open woods.
Que. to Minn., southw. to Mass. and Pa.

98. *CAREX LAXIFLORA* Lam.

C. heterosperma Wahl.; *C. anceps* Muhl.; *C. laxiflora* var. *patulifolia* (Dewey) Carey.

Common south of Saginaw Bay and rare northward to the Straits. Its preferred habitat is rich woods, especially beech-maple, but it occurs also in wet thickets and, in the northern counties, in sandy aspen woods.

N. S. to Mich., southw. to Fla. and Tex.

99. *CAREX LEPTONERVIA* Fern.

C. laxiflora var. *varians* Bailey in part; *C. laxiflora* var. *leptonervia* Fern.

Rare to infrequent in the southern counties, becoming frequent northward. It attains its best development in low rich woods but it is also found in habitats as diverse as dry wooded hills, black spruce and Thuja bogs, and limestone outcrops.

Newf. to Minn., southward to n. N. J. and Ohio (in the mountains to N. C. and Tenn.).

100. *CAREX ALBURSINA* Sheldon

C. laxiflora var. *latifolia* Boott

Common in southern Michigan; rare from Saginaw Bay northward to Emmet County. It is found in moist rich woods, especially on slopes, and less commonly in low alluvial woodlands.

Que. to Minn., southw. to Va. and Ark.

101. CAREX BLANDA Dewey

C. laxiflora var. *varians* Bailey in part; *C. laxiflora* var. *blanda* (Dewey) Boott

Very common south of Saginaw Bay in woods of all types, in thickets and infrequently in wet meadows. A single collection from north of Saginaw Bay has been seen: rich soil, Sulphur Islands near Alpena, Alpena County, C. F. Wheeler (July 12, 1895) (S).

Que. to N. Dak., southw. to Ala. and Tex.

102. CAREX GRACILESCENS Steud.

C. laxiflora Mack., not Lam., in Britt. and Brown's Illus. Flora, ed. 2; *C. laxiflora* var. *gracillima* of Gray's Man., ed. 7.

Infrequent and local in the southeastern counties, rare in the southwestern counties and apparently absent north of Saginaw Bay. Found in either low or dry woods and bordering woods in fields.

Que. to Wisc., southw. to Va. and Ark.

Section 25. GRANULARES

Staminate spike short-peduncled or sessile; the two upper pistillate spikes usually contiguous; rootstocks not long-creeping.

Perigynia elliptic-obovoid to elliptic-ovoid, 2-2.5 mm. long, 1-1.5 mm. wide, ascending, not ventricose-squarrose, rounded at the apex, abruptly very minutely beaked.....103. *C. Haleana*

Perigynia broadly ovoid to broadly obovoid, 2.5-4 mm. long, 1.5-2.5 mm. wide, soon ventricose-squarrose, tapering at the apex, minutely beaked.....104. *C. granularis*

Staminate spike long-peduncled; spikes all widely separate; rootstocks long-creeping.....105. *C. Crawei*

103. CAREX HALEANA Olney

C. granularis var. *Haleana* (Olney) Porter; *C. Shriveri* Britt.; *C. granularis* var. *Shriveri* Britt.

Common in southern Michigan, becoming infrequent northward and rare in the Upper Peninsula. It is a species of low open grounds, occurring in both sandy and marly, calcareous soils. Two collections are known from the Upper Peninsula: cedar swamp, Camp 7 near Menominee River station, Menominee County, C. A. Davis (July 19, 1905) (M); and, wet mossy pockets in conglomerate shore of Lake Superior, 1¼ miles east of Lake Glazon, Keweenaw County, F. J. Hermann 8160 (July 20, 1936) (G, H, NY).

Que. to Sask., southw. to Va., Ind. and Kans.

104. CAREX GRANULARIS Muhl.

Frequent south of Saginaw Bay, in moist or wet open habitats, usually in clay soils; infrequent in low open woods.

Vt. to Minn., southw. to Fla. and Ark.

105. CAREX CRAWEI Dewey

Frequent but local in the Lower Peninsula, in low sandy habitats chiefly on the shores of the Great Lakes. Here it is often associated with *C. Garberi* and *C. viridula* on interdunal flats and borders of beach pools. From the Upper Peninsula two collections are known: Drummond Island, Chippewa County, without collector (August 3, 1939) (M); and, wet mossy pockets in conglom-

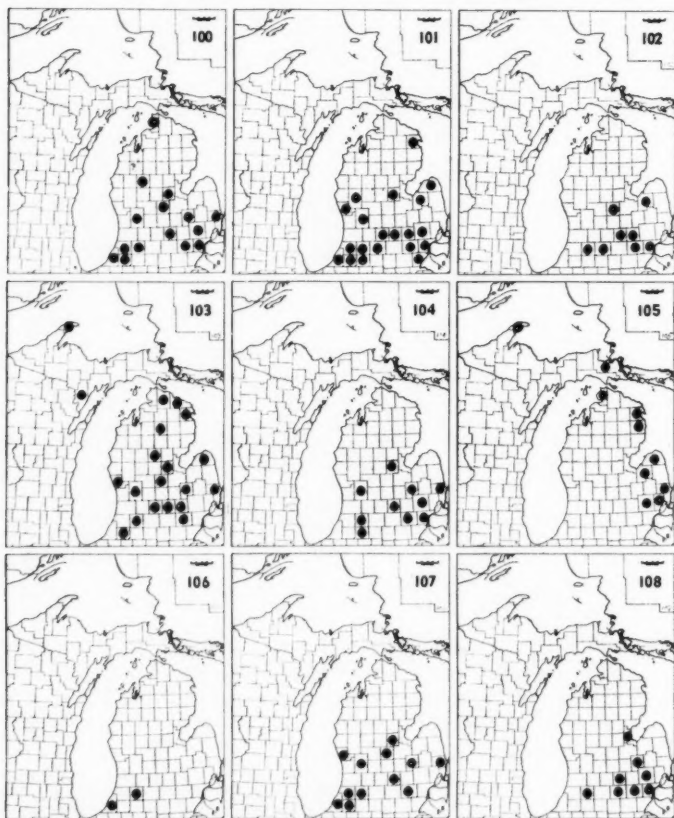
erate shore of Lake Superior, 1¼ miles east of Lake Glazon, Keweenaw County, F. J. Hermann 8162 (July 20, 1936) (H, M, NY).

Que. to Alberta and Wash., southw. to n. N. J., Ala., Tenn., Kans. and Wyo.

Section 26. OLIGOCARPAE

Bract-sheaths glabrous, the lower 0.6-2 cm. long; perigynia 4 mm. long or less; leaf-blades 2-4.5 mm. wide; culms reddish-tinged at the base.

.....106. *C. oligocarpa*
Bract-sheaths strongly hispidulous, the lower 2-6 cm. long; perigynia 4.5-5 mm.



100. *C. albursina* Sheldon; 101. *C. blanda* Dewey; 102. *C. gracilescens* Steud.; 103. *C. Haleana* Olney; 104. *C. granularis* Muhl. 105. *C. Crapei* Dewey; 106. *C. oligocarpa* Schkuhr; 107. *C. Hitchcockiana* Dewey; 108. *C. conoidea* Schkuhr.

long; leaf-blades 3-7 mm. wide; culms brownish-tinged at the base.....107. *C. Hitchcockiana*

106. CAREX OLIGOCARPA Schkuhr

Known in Michigan only from three stations in Berrien County: Sawyer, *P. E. Hebert* (May 29, 1930) (ND), Thrushwood, *P. E. Hebert* (May 29, 1931 and May 29, 1933) (ND), and, Bethany Hills, *P. E. Hebert* (June 10, 1931) (ND); and, from one station in Kalamazoo County: maple woods 1 mile west of Schoolcraft, *C. R. & F. N. Hanes* (June 1933 and July 4, 1938) (H, Hn). Its preferred habitat is rich, moist beech-maple woods. Specimens to confirm the several reports by Beal could not be found.

Vt. and Ont. to Iowa, southw. to Ala., Ky. and Tex.

107. CAREX HITCHCOCKIANA Dewey

Frequent in low rich woods south of Saginaw Bay. Often associated with *C. Jamesii*, *C. gracillima* and *C. blanda*.

Vt. and Ont. to Wisc., southw. to W. Va., Ky. and Mo.

Section 27. GRISEAE

Perigynia elliptic, 1.5 mm. wide; bract-sheaths minutely serrulate on the edges; peduncles of pistillate spikes rough; leaf-blades 2-4 mm. wide.....108. *C. conoidea*

Perigynia oblong-oval to broadly obovoid, 2-2.5 mm. wide; bract-sheaths glabrous; peduncles of pistillate spikes glabrous or nearly so; leaf-blades (2) 4-7 mm. wide109. *C. grisea*

108. CAREX CONOIDEA Schkuhr

Infrequent and local south of the Saginaw-Grand River Valleys in low open ground.

Newf. to Minn., southw. to Del., Ohio and Iowa; also in the mountains of N. C.

109. CAREX GRISEA Wahl.

Common in rich woods and thickets, along banks of streams and less frequently in wet fields, south of Saginaw Bay.

N. B. to Ont. and Minn., southw. to Ga. and Tex.

Section 28. GRACILLIMAE

Sheaths (except the lower which are dorsally somewhat hispidulous) and leaf-blades glabrous; perigynia 1.5 mm. wide.

Bracts long-sheathing; perigynia bluntly angled, obtuse at the apex; terminal spike gynaeandrous110. *C. gracillima*

Bracts sheathless; perigynia sharply angled, tapering into a triangular, often twisted, beak nearly as long as the body; terminal spike staminate111. *C. prasina*

Sheaths and often leaf-blades pubescent; perigynia 1.75-2.5 mm. wide.

Lateral spikes, as well as the terminal gynaeandrous; upper pistillate scales obtuse or acute; perigynia 2-ribbed and obscurely nerved.....112. *C. formosa*

Lateral spikes pistillate; upper pistillate scales long-cuspidate; perigynia strongly nerved113. *C. Davisii*

110. CAREX GRACILLIMA Schwein.

Common in southern Michigan, in rich moist woods, especially beech and

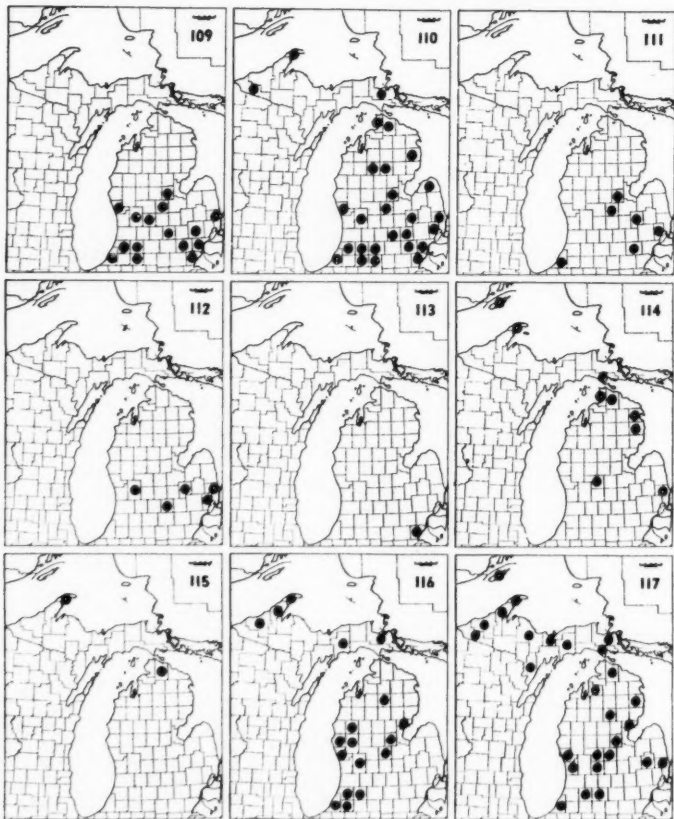
beech-maple woods; less common in damp thickets, low fields and on shores of lakes. Northward it is less frequent and here it is occasionally found in bogs as well as on wooded uplands.

Newf. to Man., southw. to Va., Ky. and Mo.

111. *CAREX PRASINA* Wahl.

Rare to infrequent south of Saginaw Bay, on springy banks along shaded streamlets and in boggy habitats in deep woods.

Que. to Mich., southw. to D. C. and Ky. (in the mountains of Ga.).



109. *C. grisea* Wahl.; 110. *C. gracillima* Schwein.; 111. *C. prasina* Wahl.; 112. *C. formosa* Dewey; 113. *C. Davisii* Schwein. & Torr.; 114. *C. castanea* Wahl.; 115. *C. Knieskernii* Dewey; 116. *C. debilis* var. *Rudgei* Bailey; 117. *C. arctata* Boott.

112. CAREX FORMOSA Dewey

Rare in rich woods, thickets and moist open ground in southern Michigan. The known distribution of this species in the state seems to be aligned with the course of the Imlay Outlet of glacial Lake Maumee.

Southwestern Que. to Wisc., southw. to Conn. and N. Y.

113. CAREX DAVISII Schwein. & Torr.

Very rare in the extreme southern part of the state. Its preferred habitats are rich alluvial beech-maple woods and moist roadside ditches. The only known collection from Michigan is: along roadside 3 miles south of Milan, Monroe County, *Betty M. Robertson* 266 (July 10, 1939) (M). The report from Keweenaw County in Beal's Flora was doubtless based upon a misidentification.

Vt. and Mass. to s. Minn., southw. to Md., Tenn. and Tex.

Section 29. SYLVATICAE

Pistillate spikes oblong-cylindric, 8-20 mm. long; leaf-sheaths and blades (at least toward the base) conspicuously pilose 114. *C. castanea*

Pistillate spikes narrowly linear or linear, 20-80 mm. long.

Leaf-sheaths, and blades toward the base, sparsely hispidulous-pilose 115. *C. Knieskernii*

Leaf-sheaths and blades glabrous.

Perigynia sessile or substipitate; scales obtuse or short acuminate, usually half the length of the perigynia or less; achenes conspicuously stipitate; broadest basal leaves 2-4.5 mm. wide 116. *C. debilis* var. *Rudgei*

Perigynia conspicuously stipitate; scales strongly cuspidate or awned, usually more than half the length of the perigynia; achenes substipitate or sessile; broadest basal leaves 5-10 mm. wide 117. *C. arctata*

114. CAREX CASTANEA Wahl.

Rare south of Saginaw Bay and infrequent northward. In Michigan it must occur very rarely, if at all, in the habitats ascribed to it by Mackenzie ("dry thickets and on banks in calcareous districts"), being found in bogs, swamps and wet, peaty meadows. The two known collections from southern Michigan are: Montcalm County, *E. F. Smith* (1883) (S); and, shaded ground near Port Huron, St. Clair County, *C. K. Dodge* (May 29, 1892) (M).

Newf. to Minn., southw. to Conn., N. Y., Mich. and Wisc.

115. Carex Knieskernii Dewey

C. castanea var. *Knieskernii* (Dewey) Mack.; *C. arctata* x *castanea* Bailey

Very rare in northern Michigan. The following collections have been seen: in low wet woods (Gorge), Douglas Lake, Cheboygan County, *H. A. Gleason* (July 17, 1935) (H); low ground and pastures, Keweenaw County, *O. A. Farwell* 612 (September 12, 1887) (M) and Clifton (August 1888) (S); and, open deciduous woods below fire lookout near Central, Keweenaw County, *M. L. Fernald & A. S. Pease* 3214 (July 7, 1934) (G, M).

N. B. and Maine to Minn., southw. to N. Y., Ont. and Mich.

116. CAREX DEBILIS Michx. var. RUDGEI Bailey

C. flexuosa Muhl.; *C. tenuis* Rudge; *C. tenuis* var. *interjecta* Britt.

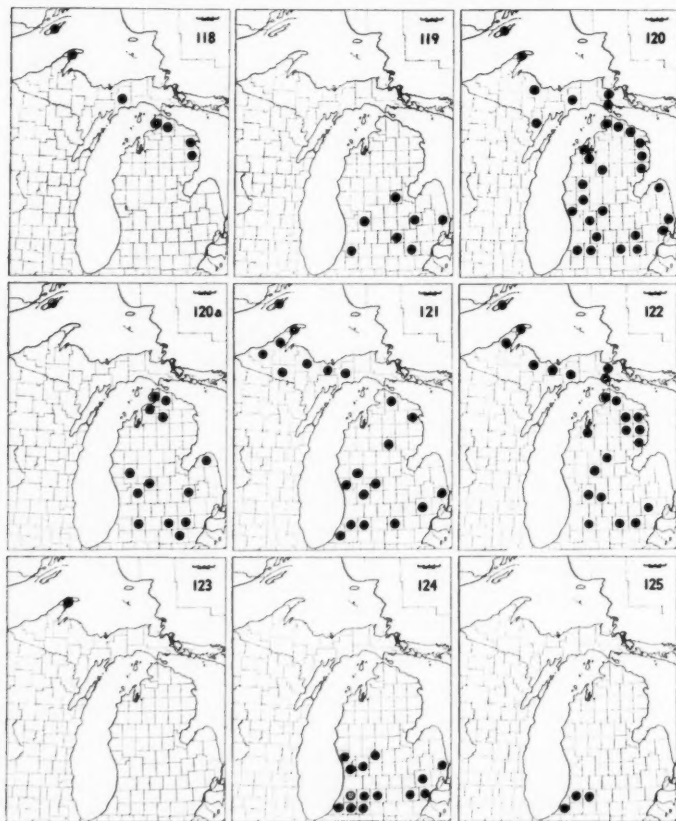
Frequent except in southeastern Michigan and in areas of sandy soils. It is found in moist, rich or boggy woods, on low borders of lakes, less frequently in wet open ground and rarely in dry or sandy woods.

Newf. to Wisc., southw. to Va. and Mo. (in the mountains to N. C. and Tenn.)

117. *CAREX ARCTATA* Boott

C. arctata var. *Faxonii* Bailey

Frequent to fairly common except in the southeasternmost counties in both rich moist and dry sandy woods; infrequent in bogs and swamps.



118. *C. capillaris* L.; 119. *C. Sprengelii* Dewey; 120. *C. viridula* Michx.; 120a. *C. viridula* f. *intermedia* (Dudley) Hermann; 121. *C. crytolepis* Mack. 122. *C. flava* L.; 123. *C. pallescens* L.; 124. *C. Swanii* (Fern.) Mack.; 125. *C. virescens* Muhl.

Newf. to Minn., southw. to Pa. and Ohio.

Section 30. CAPILLARES

118. CAREX CAPILLARIS L.

C. capillaris var. *elongata* Olney

Infrequent in northern Michigan in damp open habitats, especially in mossy pockets in conglomerate shores and in cleared Thuja bogs.

Greenl. to Alaska, southw. to Maine, n. N. Y., Mich. and in the mts, to N. Mex. and Nev.

Section 31. LONGIROSTRES

119. CAREX SPRENGELII Dewey

C. longirostris Torr.

Infrequent and local south of Saginaw Bay in moist depressions in rich, often rocky, woods. It commonly forms large colonies.

N. B. to Alberta, southw. to Del., Pa., Nebr. and Colo.

Section 32. EXTENSAE

Perigynia 2-3 mm. long, little if at all deflexed, the beak much shorter than the body; spikes oblong, 4-7 mm. wide.

Spikes 2-7, the lower often separate, the terminal usually staminate, conspicuous; pistillate scales usually reddish-tinged

.....120. *C. viridula*
Spikes 4-15, mostly densely aggregated, the terminal usually androgynous with the staminate portion very small and inconspicuous; pistillate scales usually very slightly if at all reddish-tinged.....120a. *C. viridula* f. *intermedia*

Perigynia 3.5-6 mm. long, at least the lower conspicuously deflexed, the beak equaling the body; spikes subglobose, 7-12 mm. wide.

Perigynia 3.5-4.5 mm. long, the beak smooth, pale at the tip; scales slightly if at all reddish-tinged, largely concealed by the perigynia; leaf-blades 1-3 mm. wide121. *C. cryptolepis*

Perigynia 4.5-6 mm. long, the beak serrulate, reddish-tinged at the tip; scales strongly reddish-tinged, conspicuous in the spikes; leaf-blades 3-5 mm. wide.122. *C. flava*

120. CAREX VIRIDULA Michx. (Jour. Bot. 77:301-304. 1939.)

C. Oederi var. *pumila* (Cos. & Germ.) Fern.; *C. irregularis* Schwein.

Common on wet sandy or marly borders of lakes especially around beach pools on the dunes; infrequent in marshes.

Newf. to Alaska, southw. to N. J., Ind., N. Mex., Utah and Calif.; also in Japan.

120a. CAREX VIRIDULA f. INTERMEDIA (Dudley) Hermann (in Deam, Flora of Indiana, 256. 1940.)

C. Oederi var. *prolifera* H. B. Lord; *C. Oederi* f. *intermedia* Dudley; *C. chlorophila* Mack.

Infrequent to frequent in the Lower Peninsula in the habitats of the species. It is later-flowering and -fruiting than the typical form. *C. viridula* reaches its prime in Michigan between early June and mid-July (except in the Upper Peninsula and the northern counties of the Lower Peninsula where it sometimes retains its perigynia through August) while f. *intermedia* fruits from the last week in July into October.

N. Y. to Wisc., southw. to N. J. and Ind.

121. CAREX CRYPTOLEPIS Mack.

C. flava var. *rectirostra* Gaudin, part; *C. flava* var. *graminis* Bailey

Frequent to fairly common on wet shores of lakes, either in sand, muck or marl; infrequent in swales, wet meadows, marshes and bogs.

Newf. to Minn., southw. to N. J. and Ind.

122. CAREX FLAVA L.

Frequent to fairly common in the habitats of the preceding species; more frequent in bogs and marshes than *C. cryptolepis*.

Newf. to B. C., southw. to N. J., Ind. and Mont.; also in Europe.

Section 33. VIRESCENTES

Terminal pike staminate, linear; perigynia faintly nerved 123. *C. pallescens*

Terminal spike gynaeandrous, clavate at the base; perigynia strongly nerved.

Perigynia densely pubescent; spikes 3-4 mm. thick, the lower more or less widely separate and peduncled; ligule much longer than wide.

Pistillate spikes oblong or oblong-globose, abruptly contracted or rounded at the base, the lowest 5-20 mm. long; perigynia broadly obovoid; anthers 0.8-1.6 mm. long 124. *C. Swanii*

Pistillate spikes linear, attenuate at the base, the lowest 15-40 mm. long; perigynia oblong-elliptic or narrowly obovoid; anthers 1.5-2.5 mm. long.....

..... 125. *C. virescens*

Perigynia glabrous; spikes 4-8 mm. thick, contiguous or nearly so, sessile or subsessile; ligule wider than long 126. *C. hirsutella*

123. CAREX PALLESCENS L.

Known in Michigan only from the following collections from Keweenaw County: Clifton, O. A. Farawell (August 1888) (S); wet peaty meadow, Copper Harbor, F. J. Hermann 7500 (June 17, 1936) (H, M, NY); sandy roadside, 1/2 mile southeast of Cliff, F. J. Hermann 7656 (June 24, 1936) (H); and, moist meadow, Allouez, F. J. Hermann 7672 (June 24, 1936) (S).

Newf. to Wisc., southw. to N. J., Pa. and Ill.; Eurasia.

124. CAREX SWANII (Fern.) Mack.

C. virescens var. *Swanii* Fern.

Frequent to common in southwestern Michigan; infrequent in the southeastern counties. It is found both in dry open woods and low thickets bordering swamps.

N. S. to Wisc., southw. to N. C., Tenn. and Ark.

125. CAREX VIRESCENS Muhl.

C. costellata Britt.

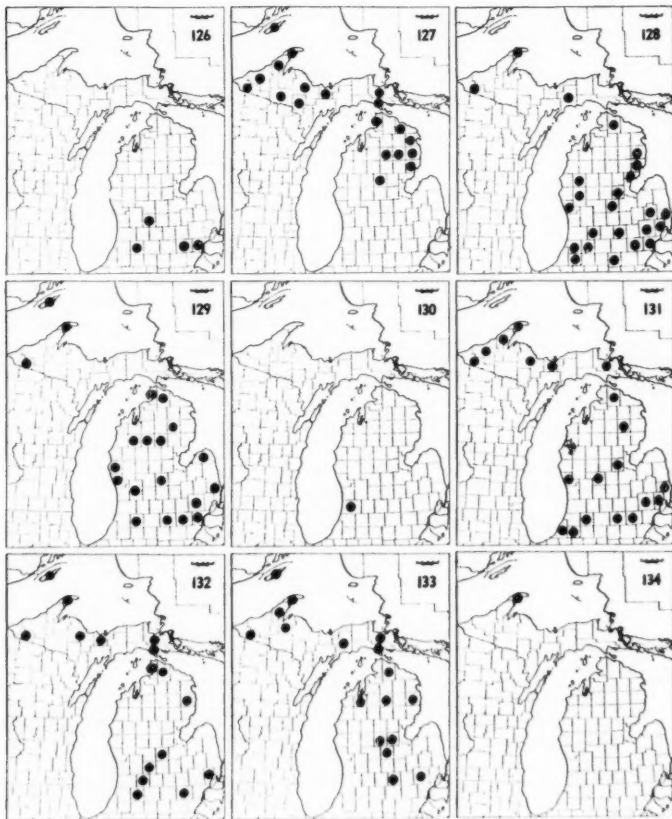
A species of dry woods and wooded bluffs (rarely of river banks and meadows) known in Michigan from only the southwestern corner of the state: Niles, Berrien County, G. L. Ames (June 14, 1869) (M); near Harbert, Berrien County, H. T. Darlington 1650 (August 22, 1917) (S); South Haven, Van Buren County, C. H. Kauffman (July 16, 1910) (M); and, low open grassy meadow, 3 miles southwest of Fulton, Kalamazoo County, C. R. & F. N. Hanes 569 (August 1, 1939) (M). The report for Detroit by Beal was based upon a collection of *C. Swanii*; his report for Keweenaw County is not plausible.

Maine to Ind., south to Ga. and Tenn.

126. *CAREX HIRSUTELLA* Mack.

C. triceps var. *hirsuta* Bailey

Rare in southern Michigan in dry open woods and on borders of low woods. The known Michigan collections are: Woodmere Cemetery, Detroit, Wayne County, without collector (July 4, 1877) (M); in oak woods in North Plains Twp., Ionia County, C. F. Wheeler (June 19, 1890) (M); border of wooded swamp northeast of Goose Lake, C. R. & F. N. Hanes 117 and 1334 (June 25, 1934) (Hn, M); and, low grassy edge of abandoned road in woods bordering



126. *C. hirsutella* Mack.; 127. *C. Houghtonii* Torr.; 128. *C. lanuginosa* Michx.; 129. *C. lasiocarpa* Ehrh.; 130. *C. hirta* L.; 131. *C. scabrata* Schwein.; 132. *C. limosa* L.; 133. *C. paupercula* Michx.; 134. *C. angarac* Steud.

Mud Lake Bog south of Barker Road, Sect. 1, Webster Twp., $1\frac{3}{4}$ miles west of Whitmore Lake, Washtenaw County, F. J. Hermann 9470 (June 1, 1938) (G, H, M, NY, S).

Maine to Mich., southw. to Ala. and Tex.

Section 34. HIRTAE

Foliage glabrous; sheaths not pilose at the mouth; staminate scales not long-ciliate; teeth of perigynium $\frac{1}{2}$ mm. long or less.

Perigynia strongly and conspicuously 15-20-ribbed; beak of perigynium nearly half the length of the body, the teeth spreading, scabrous.....127. *C. Houghtonii*

Perigynia with ribs largely obscured by the dense pubescence; beak of perigynium short (1 mm. long), the teeth erect.

Leaf-blades flat, 2-5 mm. wide; culms sharply triangular; achenes straight-apiculate128. *C. lanuginosa*

Leaf-blades involute-filiform, 2 mm. wide or less; culms obtusely triangular; achenes bent-apiculate129. *C. lasiocarpa*

Foliage soft-hairy; sheaths pilose at the mouth; staminate scales long-ciliate; teeth of perigynium more than $\frac{1}{2}$ mm. long.....130. *C. hirta*

127. CAREX HOUGHTONII Torr.

Frequent north of Saginaw Bay in open sandy or rocky habitats, especially in moist roadside ditches.

Newf. to Sask., southw. to Maine, Ont., Mich. and Minn.

128. CAREX LANUGINOSA Michx.

C. filiformis var. *latifolia* Boeckl.; *C. lasiocarpa* subsp. *lanuginosa* (Michx.) Clausen & Wahl

Common south of Saginaw Bay, becoming infrequent northward, in swamps, marshes, beach pools, swales and wet meadows, on banks of rivers and wet borders of lakes.

N. B. to B. C., southw. to Tenn., Ark., N. Mex. and Calif.

129. CAREX LASIOCARPA Ehrh.

C. filiformis Gooden., not L.

Fairly common from Roscommon County southward, becoming infrequent northward. It occurs in the habitats of the preceding species, showing a preference for boggy borders of lakes and ponds. Like *C. lanuginosa* it is often locally abundant, forming beds in marshes and quaking bogs.

Newf. to B. C., southw. to N. J., Pa., Iowa, Idaho and Wash.; also in Europe.

130. CAREX HIRTA L.

Adventive from Europe. Known in Michigan from a single collection: Shelbyville, Allegan County, O. A. Farwell 6584 (June 21, 1923) (H, M). Its usual habitats are dry fields and waste places.

Locally naturalized from P. E. I. to e. N. Y., Pa. and D. C.; also Mich. and Oreg.

Section 35. ANOMALAE

131. CAREX SCABRATA Schwein.

Infrequent to frequent in the southern counties, becoming scarce in central

Michigan and frequent in the Upper Peninsula. It is found in swales and along streamlets in rich woods, in low thickets and on borders of swamps.

N. S. and Que. to Ont. and Mich., southw. in the mountains to S. C. and Tenn.

Section 36. LIMOSAE

Pistillate scales obtuse or acute, barely exceeding the perigynia, persistent; leaf-blades more or less glaucous; plant strongly stoloniferous.....132. *C. limosa*

Pistillate scales long-attenuate with subulate tips, much exceeding the perigynia, early deciduous; leaf-blades deep green; plant loosely caespitose.....133. *C. paupercula*

132. CAREX LIMOSA L.

Infrequent in the southern counties, rare in central Michigan and frequent in the north. Its preferred habitat is open boggy or marshy borders of ponds and lakes but it is frequent, too, in sphagnum bogs.

Lab. and Newf. to Yukon, southw. to Del., Iowa, Mont. and Calif.; also in Eurasia.

133. CAREX PAUPERCULA Michx.

C. paupercula var. *irrigua* Wahl.; *C. paupercula* var. *pallens* Fern.; *C. magellanica* Boott, not Lam.

Rare in southern Michigan, probably absent from the two southernmost tiers of counties; infrequent northward and frequent to fairly common in the Upper Peninsula. It is found in sphagnum in Thuja, black spruce and Chamaedaphne bogs, and on mossy borders of pools in conglomerate shores.

Newf. to Alaska, southw. to Pa., Minn. and Utah; also in Eurasia.

Section 37. ATRATAE

Scales obtuse, shorter than or about equaling the perigynia; sheaths not filamentose.

Spikes sessile, erect, approximate; perigynia not flattened.....134. *C. angarae*

Spikes peduncled, spreading or drooping, often distant; perigynia flattened.....

.....135. *C. atratiformis*

Scales awned, much exceeding the perigynia; sheaths strongly filamentose.....

.....136. *C. Buxbaumii*

134. CAREX ANGARAE Steud. (Rhodora 41:203-205. 1939.)

C. VahlII C. A. Mey., not Schkuhr; *C. Halleri* Gunn. in part; *C. alpina* Swartz; *C. alpina* var. *inferalpina* Wahl.

A boreal species known in Michigan from a single station: cold mossy crevices at water's edge in gneiss outcrop on shore of Lake Superior near Silver Isle, Agate Harbor, Keweenaw County, F. J. Hermann 7800 (July 5, 1936) (H, M, NY, US). Reported from Isle Royale in Whitney's "Catalogue" but the specimen upon which the report was based (*A. E. Foote*, June 1868) is *C. atratiformis*.

Greenl. and Newf. to Alaska, southw. to Ont., Wisc., Wash. and in the mountains to N. Mex.; also in arctic Eurasia.

135. CAREX ATRATIFORMIS Britt.

C. ovata Rudge, not Burm.; *C. atrata* var. *ovata* (Rudge) Boott

Known in the state only from a collection from Keweenaw County: Isle Royale, *A. E. Foote* (June 1868) (M). Mackenzie gives its habitat as "sunny

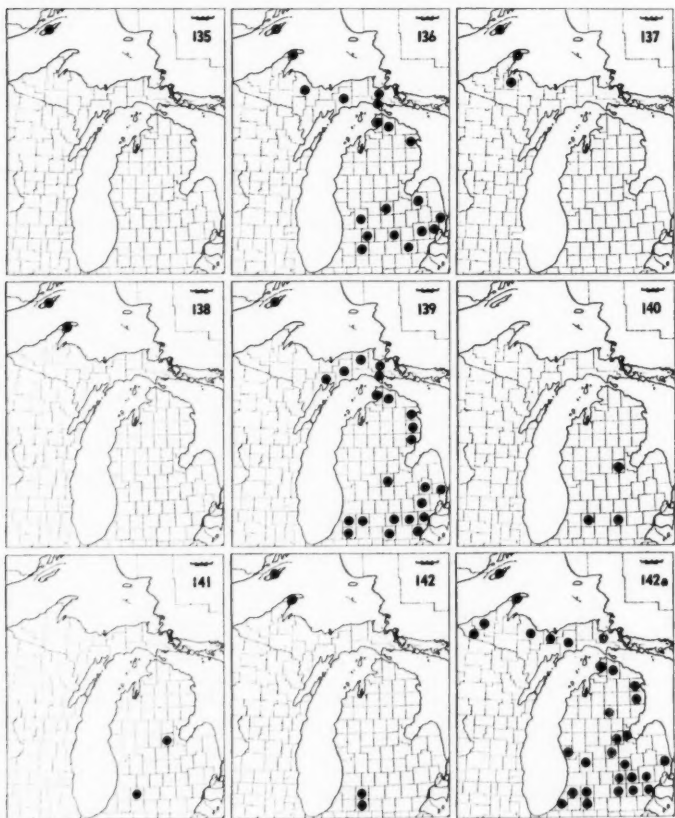
banks and meadows along streams in calcareous districts."

Labr. and Newf. to Yukon, southw. to Maine, Mich. and Alberta.

136. *CAREX BUXBAUMII* Wahl.

C. polygama Schkuhr, not Gmel.; "*C. fusca* All." of Bailey

Frequent south of Saginaw Bay; apparently rare in the jack pine plains; and infrequent northward. It is found in swampy meadows, low sandy open-



135. *C. atratifomis* Britton; 136. *C. Buxbaumii* Wahl.; 137. *C. lenticularis* Michx.; 138. *C. aquatilis* Wahl.; 139. *C. substricta* (Kükenth.) Mack.; 140. *C. Haydenii* Dewey; 141. *C. Emoryi* Dewey; 142. *C. stricta* Lam.; 142a. *C. stricta* var. *strictior* (Dewey) Carey.

ings, mossy hollows in rocky shores, sparsely wooded bogs and swales in open woods.

Newf. to Alaska, southw. to Ga., Ark., Colo. and Calif.; also in Eurasia.

Section 38. ACUTAE

Culms strongly phyllopodic (sterile shoots sometimes aphyllpodic); fertile culms surrounded at the base by the dried-up leaves of the previous year; perigynia 1.8-3.25 mm. long.

Perigynia conspicuously few-ribbed on both faces; staminate spike solitary.....137. *C. lenticularis*

Perigynia nerveless; staminate spikes two or more.

Perigynia narrowly to very broadly elliptic, broadest below the apex, 1-1.5 mm. wide138. *C. aquatilis*

Perigynia strongly obovate, broadest at the apex, 1.5-2.75 mm. wide139. *C. substricta*

Culms aphyllpodic; fertile culms all or mostly arising laterally and not surrounded at the base by the previous year's tufts of leaves; perigynia 2-2.75 mm. long.

Perigynia inflated, strongly biconvex, brownish at maturity, broadly ovate to suborbicular, 2-2.25 mm. long; pistillate scales divaricate at maturity; ligule slightly longer than wide; lower sheaths slightly if at all filamentose; stolons short, ascending; achenes suborbicular.....140. *C. Haydenii*

Perigynia not inflated, closely enveloping the achenes, unequally biconvex, green or straw-colored, 2.25-2.75 mm. long; stolons long, many, horizontal; achenes oblong to obovate.

Lower sheaths not filamentose ventrally, strongly septate-nodulose dorsally; ligule much wider than long; pistillate spikes (3) 4-5 in number, the lower 2-10 cm. long; perigynia ovate or obovate, 1.5-1.75 mm. wide.....141. *C. Emoryi*

Lower sheaths filamentose ventrally; ligule much longer than wide; pistillate spikes usually 3 in number, the lower 1-6 cm. long; perigynia elliptic to narrowly or broadly ovate, 1.5 mm. wide; pistillate scales appressed at maturity.

Leaf-sheaths glabrous ventrally, without a minute hyaline jagged-ciliate margin at the mouth142. *C. stricta*

Leaf-sheaths hispidulous ventrally (and dorsally), usually with a minute jagged-ciliate margin at the mouth; leaves usually paler green or glaucous142a. *C. stricta* var. *strictior*

137. CAREX LENTICULARIS Michx.

Rare. The known Michigan collections are all from the Keweenaw Peninsula and Isle Royale: edge of lake, Three Lakes, Baraga County, *R. R. Dreisbach* 6924 (August 15, 1930) (D); in water 2 inches deep, sandy bottom of Lake Superior, near Silver Isle, Agate Harbor, Keweenaw County, *F. J. Hermann* 1581 (Sept. 14, 1927) (H, M, S); turf by pond, Bête Gris, Keweenaw County, *M. L. Fernald & A. S. Pease* 3179 (July 5, 1934) (G, M); in water 2 inches deep, rocky edge of Lake Superior, Copper Harbor, Keweenaw County, *F. J. Hermann* 8153 (July 19, 1936) (H, M, NY); and, edge of bank, Pickerel Cove, Isle Royale, Keweenaw County, *J. B. McFarlin* 2374 (August 5, 1930) (M).

Lab. and Newf. to Mackenzie, southw. to Mass., Minn., Sask. and Iowa.

138. CAREX AQUATILIS Wahl.

C. aquatilis var. *elatior* Bab.

A boreal sedge known in Michigan only from Keweenaw County: in shallow water, sandy edge of lagoon, Bête Gris, *F. J. Hermann* 7831 (July 6, 1936) (G, H, M, NY); and, in 6-8 inches of water on edge of islands in Tobin Harbor, Isle Royale, *C. A. Brown* 3603 (August 14, 1930) (M). The numerous reports of this sedge from Michigan should be referred to other species, the greater part of them to *C. substricta* which had not been segregated at the time most of the reports were made.

Greenl. to n. Alaska, southw. to Que., n. Mich. and in the mountains to N. Mex. and Calif.; also in n. Eurasia.

139. *CAREX SUBSTRICTA* (Kükenth.) Mack.

C. aquatilis of most authors.

Fairly common in the eastern part of both the Lower and Upper Peninsulas, infrequent elsewhere, in streams and on muddy banks of creeks and lakes, in marshes, interdunal swales, wet sandy shores and bogs.

Newf. to Wash., southw. to N. J., Ind. and Mo.

140. *CAREX HAYDENII* Dewey

C. stricta var. *decora* Bailey

Rare south of Saginaw Bay. Three collections have been seen: Grass Lake, Jackson County, without collector (July 1, 1858) (S); Pawpaw Lake, Kalamazoo County, *C. R. & F. N. Hanes* 736 (June 12, 1936) (Hn); and, woods along Salt River 2½ miles south of Coleman, Midland County, *R. R. Dreisbach* 8056 (June 16, 1934) (D). Its preferred habitats are wet prairies, ditches and low clearings in open oak woods.

N. B. to Minn., southw. to N. J., Ill. and Mo.

141. *CAREX EMORYI* Dewey

Rare but locally frequent on banks of rivers, in swales, marshes and swamps south of Saginaw Bay. Known from three collections by *C. R. and F. N. Hanes* from Kalamazoo County and five collections by *R. R. Dreisbach* from Midland County. Among these are: low ground near Kalamazoo River, 1 mile east of Augusta, *C. R. & F. N. Hanes* 349 (June 16, 1939) (Hn, M); and, edge of Chippewa River at boy scout cabin 7 miles southwest of Midland, *R. R. Dreisbach* 5836 (June 15, 1928) (D, M).

N. J. and Va. to Man. and Colo., southw. to Tex. and N. Mex.

142. *CAREX STRICTA* Lam.

C. stricta var. *angustata* (Boott) Bailey

Rare. Known only from five localities: northwest portion of St. Joseph County, *C. R. & F. N. Hanes* 3849 (May 7, 1938) (Hn); boggy marsh, southwest portion of Kalamazoo County, *C. R. & F. N. Hanes* 169 (May 24, 1939) (Hn, M); marsh west of Frank Reed's, Vicksburg, Kalamazoo County, *F. W. Rapp* (May 14, 1937) (R); in sphagnum, Thuja bog southeast of Eagle Harbor, Keweenaw County, *F. J. Hermann* 8197 (July 21, 1936) (H, M, NY); and, in shallow water along creek, Brady Cove, McCargoe Cove, Isle Royale, Keweenaw County, *J. B. McFarlin* 2329 (July 30, 1930) (M).

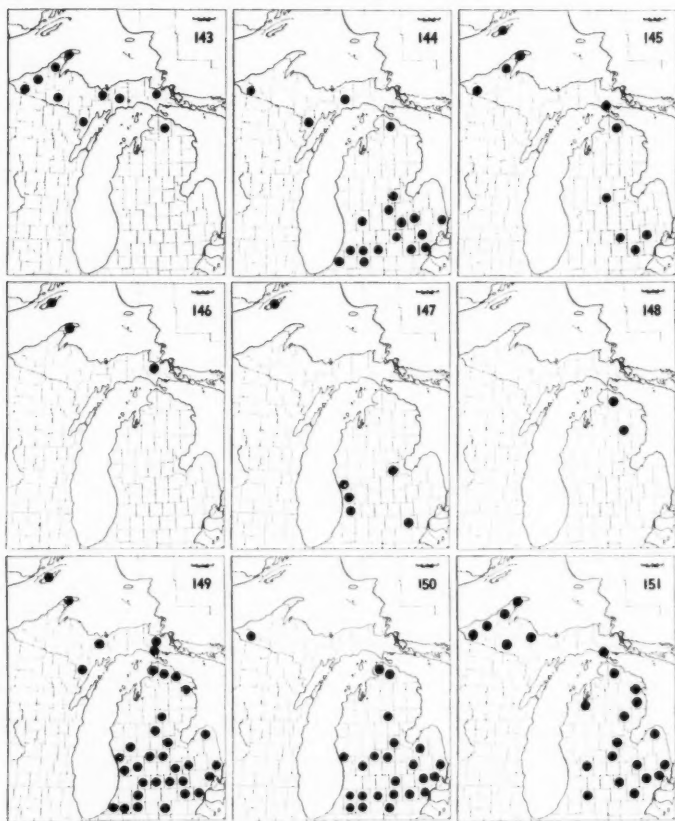
Most of the reports of this species from Michigan were based upon specimens of var. *strictior*.

Maine to N. C. and along the Coastal Plain to Texas; also locally in the Great Lakes region.

142a. *CAREX STRICTA* var. *STRICTIOR* (Dewey) Carey

C. strictior Dewey

Common in marshes and open swamps, in roadside ditches, on banks of creeks and on boggy borders of ponds and lakes. Often locally abundant forming extensive beds sometimes known as "sedge meadows."



143. *C. gynandra* Schwein.; 144. *C. crinita* Lam.; 145. *C. pauciflora* Lightf.;
146. *C. Michauxiana* Böck.; 147. *C. folliculata* L.; 148. *C. Schweinitzii* Dewey;
149. *C. hystericina* Muhl.; 150. *C. comosa* Boott; 151. *C. Pseudo-Cyperus* L.

Que. to Minn., southw. to D. C. (in the mountains to N. C. and Tenn.) and Iowa.

Section 39. CRYPTOCARPAE

Sheaths rough-hispidulous; lower pistillate scales rounded to truncate or tapering into an awn 143. *C. gynandra*
 Sheaths smooth; lower pistillate scales emarginate, abruptly contracted into an awn. 144. *C. crinita*

143. CAREX GYNANDRA Schwein.

C. crinita var. *gynandra* (Schwein.) Schwein. & Torr.

Frequent to fairly common in the Upper Peninsula in wet habitats of all types. In the Lower Peninsula it is known only from three collections (*L. E. Smith* 74; *J. H. & L. S. Ehlers* 2296; and *F. J. Hermann* 1777) from Cheboygan County.

Along the Atlantic coast this species is commoner southward than *C. crinita*, while inland the reverse is true, *C. gynandra* in Michigan being apparently confined to the north and *C. crinita* being frequent only south of Saginaw Bay.

Newf. to Wisc., southw. to Fla. and La.

144. CAREX CRINITA Lam.

Common in swamps, swampy woods and thickets, in swales, bogs, ditches and on low borders of lakes.

Que. to Minn., southw. to N. C.

Section 40. ORTHOCERATES

145. CAREX PAUCIFLORA Lightf.

Rare in the southern counties and infrequent in northern Michigan. It is found in *Chamaedaphne*, *Thuja*, black spruce and tamarack bogs, always in sphagnum.

Newf. to Alaska, southw. to Conn., Pa., Minn. and Wash.

Section 41. FOLLICULATAE

Leaf-blades 2-4 mm. wide; bract-sheaths concave at the mouth; staminate spike 6-15 mm. long, sessile or very short-peduncled 146. *C. Michauxiana*
 Leaf-blades 4-15 mm. wide; bract-sheaths prolonged at the mouth; staminate spike 12-30 mm. long, peduncled 147. *C. folliculata*

146. CAREX MICHAUXIANA Böck.

C. abacta Bailey.

Rare in bogs and marshy fields in the Upper Peninsula. Represented only from two counties: bogs near small lake, Whitefish Point, Chippewa County, *C. K. Dodge* (June 18, 1914) (M); spruce-tamarack bog, $3\frac{1}{4}$ miles northwest of Homestead, Sugar Island, Chippewa County, *F. J. Hermann* 7220 (September 6, 1935) (H, M); beaver pond, Clifton, Keweenaw County, *O. A. Farwell* (August 10, 1888) (S); marshy field $1\frac{1}{2}$ miles southeast of Eagle River, Keweenaw County, *F. J. Hermann* 8137 (July 17, 1936) (H, NY, US); and, Hidden Lake, Tobin Harbor, Isle Royale, Keweenaw County, *C. A. Brown* 3599 (August 14, 1930) (M).

Newf. to Ont., southw. to N. H., N. Y., Pa. and Mich.; also in e. Asia.

147. *CAREX FOLLICULATA* L.

Infrequent in wet woods, swampy dunes and low shores of lakes south of Saginaw Bay; not known from central Michigan, and rare in the Upper Peninsula. The two collections seen from north of Saginaw Bay are: swampy open or slightly shaded ground near Emerson, Chippewa County, C. K. Dodge (August 27, 1914) (M); and, Isle Royale, Keweenaw County, C. A. Davis (1905) (M). No specimens could be found to confirm Beal's reports from Flint and Macomb County.

Newf. to Wisc., southw. to D. C., Ind. and in the mountains to N. C. and Tenn.

Section 42. PSEUDO-CYPERI

Teeth of perigynia not over 0.5 mm. long; perigynia suborbicular in cross-section, inflated, membranaceous, spreading; culms stoloniferous; ligule not longer than wide.

Staminate scales acute to cuspidate; pistillate scales not ciliate; stolons well-developed, numerous 148. *C. Schweinitzii*

Staminate scales with rough awns; pistillate scales ciliate-serrulate above; stolons few 149. *C. hystricina*

Teeth of perigynia 0.5 mm. long or more; perigynia flattened-triangular, scarcely inflated, coriaceous, more or less reflexed; culms not stoloniferous; ligule much longer than wide.

Teeth of perigynia recurved-spreading, 1.2-2 mm. long; beaks of perigynia (exclusive of the teeth) 1.5-2.2 mm. long, equaling or longer than the bodies; perigynia 6 mm. long 150. *C. comosa*

Teeth of perigynia erect or slightly spreading, 0.5-1 mm. long; beaks of perigynia (exclusive of the teeth) averaging 1 mm. long, shorter than the bodies; perigynia 4-5 mm. long 151. *C. Pseudo-Cyperus*

148. *Carex Schweinitzii* Dewey

A rare species, known in the state from only three localities: Oscoda County, without collector (June 15, 1888) (S); the Gorge, Cheboygan County, L. E. Smith 276 (June 27, 1920) (M); boggy banks of Carp Creek on west side of Burt Lake, Cheboygan County, J. H. & L. S. Ehlers 2388 (June 29, 1923) (M); and, C. O. Erlanson 78 (June 22, 1924) (H, M). Specimens could not be found to corroborate Beal's report of Prof. Bailey's collection from Crawford County. A very local sedge throughout its range.

Vt. to s. Ont. and n. Mich., southw. to Conn., N. J., N. C., Tenn. and Mo.

149. *CAREX HYSTRICINA* Muhl.

C. hystricina var. *Dudleyi* Bailey

Very common south of Saginaw Bay and frequent northward. It occurs in wet habitats of all types, especially on shores of lakes, banks of creeks and along marshy roadsides.

A form in which the terminal spike is gynaeandrous rather than staminate has been seen in three collections: bank of Pine River, Alma, Gratiot County, C. A. Davis (July 20, 1895) (S); Keweenaw County, O. A. Farwell (1886)

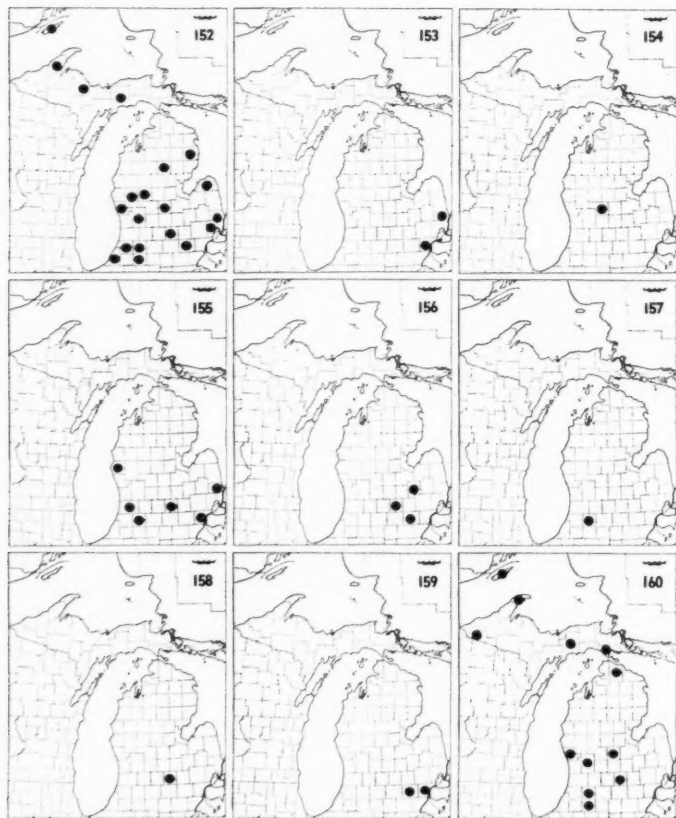
(S); and, sandy border of roadside ditch, 1½ miles east of Central, Keweenaw County, F. J. Hermann 8018 (July 15, 1936) (H).

Que. to Wash., southw. to Va., Ky., Tex. and Calif.

150. CAREX COMOSA Boott

C. Pseudo-Cyperus var. *americana* Hockst.

Common south of Saginaw Bay on low borders of lakes, open banks of streams, and in swamps and swales; infrequent northward. In the Upper



152. *C. riparia* var. *lacustris* (Willd). Kük. & Schum.; 153. *C. hyalinolepis* Steud.; 154. *C. subimpressa* Clokey; 155. *C. atherodes* Spreng.; 156. *C. trichocarpa* Muhl.; 157. *C. Frankei* Kunth; 158. *C. typhina* Michx.; 159. *C. squarrosa* L.; 160. *C. vesicaria* L.

Peninsula known only from Gogebic County: lake region, *H. T. Darlington* 2442 (August 1919) (S), and, edge of Bass Lake, *H. T. Darlington* 2642 (August 14, 1919) (M).

Que. to Minn., southw. to Fla. and La.; also locally in the Pacific states.

151. CAREX PSEUDO-CYPERUS L.

Frequent throughout the state in swamps, marshes and bogs and on wet borders of lakes.

Newf. to Sask., southw. to Conn., N. Y., n. Ind. and Minn.; also in Eurasia.

Section 43. PALUDOSAE

Beaks of perigynia much shorter than the body, the teeth short, about 0.5 mm. long, erect or nearly so; foliage glabrous.

Perigynia glabrous.

Mature perigynia strongly nerved; fertile culms aphyllopodic, strongly reddish-tinged at the base, the lower sheaths filamentose ventrally; ligule at least twice as long as wide.....152. *C. riparia* var. *lacustris*

Mature perigynia impress-nerved; fertile culms phyllopodic, less strongly or not at all reddish-tinged at the base, the lower sheaths not filamentose ventrally; ligule shorter or moderately (less than 1½ times) longer than wide.....153. *C. hyalinolepis*

Perigynia hairy, the ribs mostly hidden by the short dense pubescence.....154. *C. subimpressa*

Beaks of perigynia (including teeth) nearly as long as the body, the teeth prominent, 1-3 mm. long, erect or widely spreading.

Perigynia glabrous; leaf-sheaths pubescent; at least the lower leaf-blades sparsely pubescent below toward the base.....155. *C. atherodes*

Perigynia hairy; leaf-sheaths and blades glabrous.....156. *C. trichocarpa*

152. CAREX RIPARIA Curtis var. LACUSTRIS (Willd.) Kükenth.

Carex lacustris Willd.

Frequent in southern Michigan in marshes, swamps and on boggy borders of lakes; infrequent northward.

Que. to Sask., southw. to Va. and Iowa.

153. CAREX HYALINOLEPIS Steud.

C. riparia var. *impressa* S. H. Wright; *C. impressa* (S. H. Wright) Mack.

Southeastern Michigan; very rare. The known collections are: Detroit, Wayne County, without collector (July 4, 1877) (M); Belle Isle, Detroit, Wayne County, *O. A. Farwell* (1894) (M); and, wet places near Port Huron, St. Clair County, *C. K. Dodge* (May 27, 1899) (M). It is a species of swales, wet depressions in open woods, flood plains, marshy borders of ponds and roadside ditches.

N. J. to Ont. and Nebr., southw. to Fla. and Tex.

154. CAREX SUBIMPRESSA Clokey

C. lanuginosa x *impressa* Clokey

A very local sedge known in Michigan from a single collection: low wet meadow, Cedar Lake, Montcalm County, *C. A. Davis* (June 10, 1897) (H, M).

Mich., Ind. and Ill.

155. *CAREX ATHERODES* Spreng.

C. trichocarpa var. *imberbis* Gray; *C. trichocarpa* var. *aristata* (R. Br.) Gray; *C. aristata* R. Br.

Infrequent and local in marshes and boggy lake shores in southern Michigan. No evidence was found to substantiate Beal's statement that it occurs "northward to Lake Superior."

Ont. to Yukon, southw. to N. Y., Ind., Mo., Kans., Utah and Oreg.; also in Eurasia.

156. *CAREX TRICHOCARPA* Muhl.

Rare in southeastern Michigan. The known collections are: ditch bordering gravelly embankment of M. C. R. R. 23/4 miles east of Ann Arbor, Washtenaw County, F. J. Hermann 9188 (September 5, 1937) (M) and 9474 (June 2, 1938) (G, NY); bank west of old Botanical Laboratory site, East Lansing, Ingham County, C. F. Wheeler (June 24, 1893) (M); and, along ditch, Flint, Genesee County, H. Hasselbring (June 20, 1929) (H). The specimen forming the basis for Beal's report from Macomb County could not be located.

Que. and Vt. to Minn., southw. to N. J., Ind. and Iowa.

Section 44. *SQUARROSAE*

- Perigynia shorter than the rough-awned scales, 14-20-ribbed; terminal spike usually staminate, narrowly linear, small (0.5-2.5 cm. long); ligule slightly, if at all, longer than wide; achenes about 1.5 mm. long.....157. *C. Frankii*
- Perigynia much longer than the scales, several-ribbed above; terminal spike gynae-candrous; ligule much longer than wide; achenes 2.2-3 mm. long.
- Beaks of perigynia mostly appressed-ascending; spikes oblong-cylindric; achenes obovoid, their sides concave; pistillate scales mostly blunt; style straight below.....158. *C. typhina*
- Beaks of perigynia widely radiating; spikes oval or oblong-oval; achenes linear-oval, their sides almost flat; pistillate scales acute to short-awned; style strongly curved or bent below.....159. *C. squarrosa*

157. *CAREX FRANKII* Kunth

C. stenolepis Torr., not Less.

A southern species known in the state from a single collection: low open woodland, Sect. 33, Climax Twp., Kalamazoo County, C. R. & F. N. Hanes 429 (July 7, 1939) (H, M, US).

Pa. and N. Y. to Ill. and Kans., southw. to Ga. and Tex.; also in S. A.

158. *CAREX TYPHINA* Michx.

C. typhinoides Schwein.

A sedge of low flat woods, marshes, swamps and borders of ponds, known in Michigan only from Ingham County: Lansing, L. H. Bailey (July 1, 1886) (S); and, low place, Potter Park, Lansing, C. Billington (September 20, 1924) (M).

Que. to Wisc. and Iowa, southw. to Ga. and La.

159. *CAREX SQUARROSA* L.

Rare in southeastern Michigan in swampy woods and wet borders of ponds and creeks. The collections seen are: Grosse Isle, Wayne County, M. H. Clark (without date) and C. K. Dodge (July 22, 1911) (M); Detroit, Wayne

County, *A. B. Lyons* (June 15, 1877 (M); and, Washtenaw County (without collector or date) (M). Beal's report for Lansing was based upon Bailey's collection of *C. typhina*; the basis of his Hubbardston report could not be found; and the report from Keweenaw County was doubtless based upon a misidentification.

Que. to Wisc. and Nebr., southw. to N. C. and Ark.

Section 45. VESICARIAE

Pistillate scales not rough-awned.

Pistillate spikes oblong to cylindric, 17-many-flowered; leaf-blades flat or their margins somewhat revolute.

Perigynia not reflexed; bracts moderately exceeding the inflorescence.

Achenes not excavated on one side; perigynia 2.5-3.5 mm. wide.

Culms sharply triangular below the spikes, rough; perigynia appressed or ascending; teeth of perigynia long or the perigynia gradually (long)-beaked; lower sheaths fragile, becoming strongly filamentose; ligule much longer than wide; rootstocks without long horizontal stolons160. *C. vesicaria*

Culms bluntly triangular below the spikes, smooth; perigynia ascending or squarrose at maturity; teeth of perigynia short or the perigynia abruptly (short)-beaked; lower sheaths not fragile, not becoming filamentose; ligule slightly if at all longer than wide; rootstocks with long horizontal stolons161. *C. rostrata*

Achenes deeply excavated on one side; perigynia 5-6.5 mm. wide162. *C. Tuckermanni*

Perigynia, at least the lower, reflexed or widely spreading, somewhat falcate;

bracts many times exceeding the inflorescence163. *C. retrorsa*

Pistillate spikes globose or short-oblong, 3-18-flowered; leaf-blades involute164. *C. oligosperma*

Pistillate scales rough-awned165. *C. lurida*

160. CAREX VESICARIA L.

Including *C. vesicaria* var. *jejeuna* Fern. and *C. vesicaria* var. *monile* (Tuckerm.) Fern. (*C. monile* Tuckerm.)

Infrequent south of Saginaw Bay and in northern Michigan; apparently absent from the central part of the state. It is found in swamps, bogs, wet thickets and swales.

Newf. to B. C., southw. to Del., Ind., Mo., N. Mex. and Calif.; also in Eurasia.

161. CAREX ROSTRATA Stokes

C. utriculata Boott; *C. rostrata* var. *utriculata* (Boott) Bailey.

Common in swamps, marshes, swales and bogs, and on low borders of streams and lakes.

Greenland to Alaska, southw. to Del., W. Va., Ind., S. Dak., N. Mex. and Calif.; also in Eurasia.

162. CAREX TUCKERMANI Boott

Fairly common in low woods and swales, frequent in bogs, on boggy borders of lakes, and infrequent in wet open habitats. Possibly absent from Houghton and Keweenaw Counties.

N. B. to Minn., southw. to N. J., Ind. and Iowa.

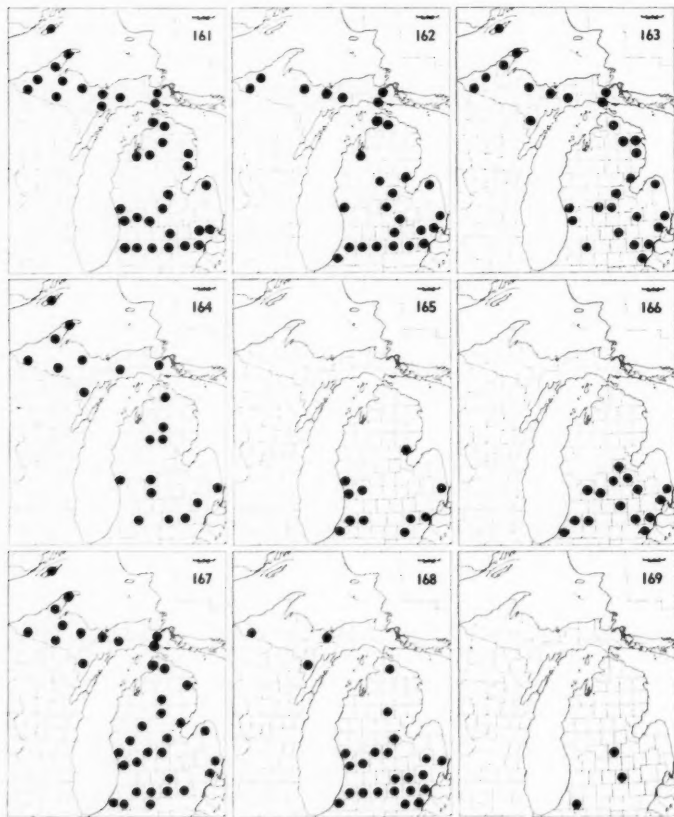
163. *CAREX RETRORSA* Schwein.*C. retrorsa* var. *Hartii* Gray

Frequent throughout the state, becoming fairly common northward, in bogs, swamps and on springy or marshy banks of streams.

Que. to B. C., southw. to N. J., Ind., Iowa, Colo. and Oreg.

164. *CAREX OLIGOSPERMA* Michx.

Infrequent in southern Michigan, becoming frequent northward, generally in sphagnum, in tamarack and *Chamaedaphne* bogs, but occurring also on



161. *C. rostrata* Stokes; 162. *C. Tuckermanni* Boott; 163. *C. retrorsa* Schwein; 164. *C. oligosperma* Michx.; 165. *C. lurida* Wahl.; 166. *C. Grayii* Carey; 167. *C. intumescens* Rudge and var. *Fernaldii* Bailey; 168. *C. lupulina* Muhl.; 169. *C. lupuliformis* Sartwell.

marshy borders of ponds, in swales and swamps.

Newf. to Mack., southw. to Mass., Pa. and Ind.

165. CAREX LURIDA Wahl.

C. lurida var. *flaccida* Bailey

Infrequent to locally frequent from Muskegon and St. Clair Counties southward; north of this known only from Arenac County. It is found in swamps, ditches, low woods and wet habitats of all types. The report for Keweenaw County in Beal's Flora was doubtless based upon a misidentification.

N. S. to Minn., southw. to Fla., Tex. and Vera Cruz.

Section 46. LUPULINAE

Pistillate spikes globose to short-ovoid; style straight or the bend remote from the achene.

Perigynia radiating in all directions, cuneate at the base, subcoriaceous, usually somewhat hispidulous; staminate spike usually sessile or short-peduncled; achenes obscurely trigonous, almost suborbicular in cross-section, the angles inconspicuous 166. *C. Grayii*

Perigynia ascending, rounded at the base, membranaceous, smooth and shining; staminate spike normally long-peduncled; achenes with blunt angles but conspicuously trigonous.

Perigynia broadly ovoid, about half as broad (5-8 mm.) as long.....

..... 167. *C. intumescens*

Perigynia narrowly ovoid, one-fourth to one-third as broad (3.5-5 mm.) as long 167a. *C. intumescens* var. *Fernaldii*

Pistillate spikes oblong to cylindric; style abruptly bent immediately above the achene.

Achenes conspicuously longer than wide, the angles not prominently knobbed, the sides shallowly concave; pistillate spikes short-oblong to oblong-cylindric. 168. *C. lupulina*

Achenes not longer than wide, the angles prominently knobbed, the sides deeply concave; pistillate spikes cylindric or oblong cylindric..... 169. *C. lupuliformis*

166. CAREX GRAYII Carey

C. Grayii var. *hispidula* Gray; *C. Asa-Grayi* Bailey

Infrequent to locally frequent south of Saginaw Bay in low rich woods; occasional on borders of swamps and in wet open habitats.

Vt. to Wisc., southw. to Ga., Tenn. and Mo.

167. CAREX INTUMESCENTS Rudge

Frequent to fairly common south of Saginaw Bay; infrequent to rare northward. It is found in low woods and Thuja bogs and rarely in wet habitats in the open.

N. H. to Wisc., southw. to Fla. and Tex.

167a. CAREX INTUMESCENTS var. FERNALDI Bailey

Infrequent to frequent northward to Saginaw Bay; frequent to common in the Upper Peninsula and the northernmost counties of the Lower Peninsula. Its habitats are those of the species but it is more frequently found in swales, marshes and other open habitats than is the typical form.

Newf. to Keewatin, southw. to Mass., N. Y., Ind., Ill. and in the mountains to N. C.

168. *CAREX LUPULINA* Muhl.*C. lupulina* var. *pedunculata* Gray

Fairly common to locally common south of Saginaw Bay; infrequent northward. It occurs in a diversity of wet habitats, such as swamps, marshes, low woods and thickets, swales and ditches.

N. S. to Minn., southw. to Fla. and Tex.

169. *CAREX LUPULIFORMIS* Sartwell

Rare in swampy woods and *Cephalanthus* swamps south of Saginaw Bay. Only three collections have been seen from the state: wet woods, Silver Creek, Cass County, *H. S. Pepon* 607 (August 1908) (S); swamp northwest of Michigan Agricultural College, East Lansing, Ingham County, *C. F. Wheeler* (July 1891) (S); and, Alma, Gratiot County, *C. A. Davis* (June 28 and July 18, 1893) (M).

Vt. to Minn., southw. to Del., La. and Tex.

EXCLUDED SPECIES

1. *CAREX RETROFLEXA* Muhl.—Beal reports this species as "Frequent. S." Mackenzie (N. Am. Fl. 18:44. 1931.), in outlining its general range, says "Vermont and Massachusetts to Ontario and Michigan," but Michigan is not included in his enumeration of states from which he saw specimens. Although the species is known from Indiana and may occur in the southernmost counties of Michigan no specimens could be found in herbaria to corroborate the reports.

Vt. and Mass. to Ont. and Ill., southw. to Fla. and Tex.

2. *CAREX RADIATA* (Wahl.) Dewey (*C. rosea* var. *radiata* (Wahl.) Dewey)—Beal states that this species occurs in "Dry woods. Frequent. Th." This report was doubtless based upon a misapplication of the name to *C. rosea*. Mackenzie (N. Am. Fl. 18:47. 1931.) also records *C. radiata* from Michigan. This report was apparently based upon a collection in the herbarium of the New York Botanical Garden by W. A. Brotherton from Rochester, Mich., in 1898. This specimen was determined as *C. radiata* (Dewey) Small by Mackenzie. The collection is overripe but since the few remaining perigynia show the stigmas to be uniformly straight it may be safely referred to *C. rosea*.

Que. and Maine to Ohio, southw. to N. C. and Tenn.

3. *CAREX GRAVIDA* Bailey—Reported from Berrien County by Hebert (Am. Midl. Nat. 15:327. 1934). The report was based upon two collections in the herbarium of the University of Notre Dame, one of which is *C. gravida* var. *Lunelliana* and the other *C. alopecoidea*.

Southwestern Ont. and Ohio to N. D. and Wyo.

4. *CAREX BRACHYGLOSSA* Mack. (*C. annectens* var. *xanthocarpa* (Bickn.) Wieg.)—Reported for Michigan by Mackenzie (N. Am. Fl. 18:69. 1931.) but no specimens from the state could be found at the herbarium of the New York Botanical Garden or elsewhere.

Maine to Iowa, southw. to Va. and Kans.

5. *CAREX CONJUNCTA* Boott—Reported by Beal from Manistee and from Van Buren County and by Walpole from Washtenaw County but specimens to substantiate the reports could not be located. Mackenzie (N. Am. Fl. 18:82. 1931.) ascribes the species to Michigan and his report was apparently based upon two Michigan collections in the herbarium of the New York Botanical Garden referred by him to *C. conjuncta*. One of these, collected by D. Clark at Flint in 187-, is *C. alopecoidea*; the other, collected by W. A. Brotherton at Rochester in 1898, is *C. stipata*. It has been reported also from Berrien County by P. E. Hebert (Am. Midl. Nat. 15:327. 1934.) but the specimen forming the basis of the report (in herbarium of the University of Notre Dame) is *C. alopecoidea*.

N. Y. and N. J. to D. C., westw. to S. D. and Kans.

6. *CAREX PRATICOLA* Rydb. (*C. pratensis* Drej, not Hose).—In his "Michigan Flora" Beal includes this boreal species, giving a single citation: "Pic River, Lake Superior, C. Loring;" but the Pic River is in Thunder Bay District, Ontario. Brown repeats Cooper's report from Isle Royale (Ann. Rept. Mich. Acad. Sci. 16:109-131. 1914.) and Mackenzie records it from Michigan and from "Isle Royale, Manitoba" (N. Amer. Fl. 18:141. 1931.) but no Michigan material could be found in the Michigan herbaria or in the herbarium of the New York Botanical Garden.

Greenl. to Yukon and Alaska, southw. to Que., Colo. and n. Calif.

7. *CAREX TINCTA* Fern.—Mackenzie (N. Amer. Fl. 18:149. 1931.) includes Michigan in the range of this species, but does not include it among the states from which he saw specimens.

No collections of the species from the state could be located in the herbarium of the New York Botanical Garden. The basis of the report may have been a collection by C. K. Dodge in the herbarium of the University of Michigan which Mackenzie had referred to *C. tincta*, but the specimen is immature *C. tribuloides*.

N. B. and Maine to Alberta, southw. to Conn.

8. *CAREX WILLDENOWII* Schkuhr—No specimen could be found to corroborate Beal's report of this species ("Bear Lake, Van Buren County, E. J. Hill. Rare.")

Ga. to Tex., northw. to Vt., Ohio and Ont.

9. *CAREX AMPHIBOLA* Steud. (*C. grisea* var. *angustifolia* Boott)—The only report for this species is by Hebert (Am. Midl. Nat. 15:328. 1934.) The specimen forming the basis of the report (University of Notre Dame Herbarium) is *C. oligocarpa*.

Fla. to Tex., northw. to N. J. and Ind.

10. *CAREX GLAUCODEA* Tuckerm.—Beal's report (Keeler, Van Buren County. Pepon.) is not supported by a specimen so far as can be found. Reported by Hermann from Washtenaw County (Papers Mich. Acad. Sci.

21:85. 1936.) but this report was based upon a sterile specimen which is probably referable to *C. laxiculmis*.

Mass. to Ont. and Ill., southw. to N. C. and Ark.

11. *CAREX AESTIVALIFORMIS* Mack.—The basis of Mackenzie's report of this eastern species from Michigan (N. Amer. Fl. 18:282. 1935.) is unknown. No Michigan material was found in the Michigan herbaria, in the herbarium of the New York Botanical Garden or the U. S. National Herbarium.

N. H. to Del., westw. to N. Y.

12. *CAREX CAROLINIANA* Schwein. (*C. triceps* var. *Smithii* Porter)—Reported by Beal as having been collected at Lapeer by Miss M. Owens, but no specimen could be located.

N. J. and Pa. to N. C., Ind. and Tex.

13. *CAREX BUSHII* Mack.—Mackenzie (N. Am. Fl. 18:325. 1935.) ascribes this southern species to Michigan apparently upon the basis of a single sheet in the herbarium of the New York Botanical Garden (Clifton, Keweenaw County, O. A. Farwell, August 1886). The specimen was distributed as *C. abbreviata* Schw. in. but was correctly referred to *C. Bushii* by Mackenzie. The sheet must certainly bear a mixed label since Keweenaw County is 650 miles north of the known range of *C. Bushii* and its flora shows no affinities with an austral floristic element.

Mass. to Kans., southw. to Va., Miss. and Tex.

14. *CAREX FLACCA* Schreb. (*C. glauca* Scop.)—Beal reports a collection of this European species by Farwell from Belle Isle, Wayne County, but no specimen was found in either of the state herbaria.

Naturalized in meadows, N. S., Que. and Ont.; St. Croix; Jamaica. Widely distributed in Europe, w. Asia and n. Africa.

15. *CAREX CONCOLOR* R. Br.—An arctic species reported from Isle Royale by Brown. Specimens to substantiate the report could not be found.

Greenl. to Alaska, southw. to the mountains of N. H. and n. N. Y.

16. *CAREX BAILEYI* Britton (*C. lurida* var. *gracilis* Bailey)—In his "Additions to the Michigan Flora" Beal reports a collection of this eastern species from Van Buren County by Pepoon. No specimen could be located and the occurrence of the species in Michigan is highly improbable.

N. H. to N. Y., southw. in the mountains to Va. and Tenn.

DIVISION OF PLANT EXPLORATION AND INTRODUCTION,
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A Systematic Study of *Triteleia*

Robert F. Hoover

In a definition of *Brodiaea* (Hoover, 1939) preparatory to a general revision, a group of species was excluded under the name *Triteleia*, with the statement that a previous delimitation of that genus by Greene (1886) was accepted. A study of extensive material of the species which have been referred to *Brodiaea* showed that *Triteleia* as well as *Brodiaea* was in need of revision. Most of the important flower characters are readily observable in herbarium specimens of *Triteleia*, so that identification of such material is not so difficult as in *Brodiaea*. Difficulties of classification in *Triteleia* appear to result mainly from incomplete understanding of the significant specific characters. Although my facilities for field work have been rather limited in comparison with the geographic range of the genus, it has been possible to study most of the species and varieties under cultivation. The results here presented are accordingly based primarily on observation of living plants.

When the genus *Triteleia* was first described by Lindley (1830), three species were included: (1) *T. bivalvis*, a South American species, (2) *T. uniflora*, also South American, and (3) *T. grandiflora*, which has been regarded by North American botanists as the type of the genus. The identity of the type species is important in determining the application of the generic name, because the North American and South American species are not actually of the same genus. If the usual procedure of taking the first listed species as the type is to be followed, the North American plants can not be known as *Triteleia*. However, when the discussion accompanying the original description is taken into account, it appears that *T. grandiflora* was intended to be the primary basis of the proposed genus. According to Lindley, the genus was "marked in Mr. Douglas's papers *Triteleia*, which we suspect is a name furnished to him by Dr. Hooker." The plant of Douglas naturally would be *T. grandiflora*, which he collected, rather than one of the South American species which Lindley included in the same genus. Some of the significant differences separating the North American from the South American plants have been reviewed recently by Hoover (1939). Accordingly, the name *Triteleia* is here used for an exclusively North American group of species.

Triteleia as treated in this revision appears to have been recognized as a single distinct genus only by Greene (1886). It is therefore desirable to present in full the evidence on which is based my understanding of the limits of the genus. The group as a whole was first referred to *Milla* by Baker (1871). *Milla biflora* Cav., the Mexican species on which that genus was originally based, differs from all species of *Triteleia* in several significant features, among which may be mentioned the brown membranous bulb-coats, apparently non-carinate leaves, consistently few-flowered umbel, unjointed pedicels, large spreading stigma, and strongly flattened seeds. Because of these differences, Watson

(1879) removed *Triteleia* from *Milla* and placed it in *Brodiaea*, where it has been retained by many recent authors. Greene (1886) pointed out the natural position of *Triteleia* as a genus, but the morphological characters given as the basis for its separation from *Brodiaea* were seemingly inadequate. In defining *Brodiaea*, Hoover (1939) listed some additional features which distinguish *Triteleia* from that genus.

The principal argument for the inclusion of *Brodiaea* and *Triteleia* in the same genus appears to be the presence in both groups of a perianth-tube. In *Triteleia hyacinthina* and *T. Lemmonae*, however, the perianth-tube is very short, while in some species of *Allium* the perianth-segments are joined at the base. It is therefore evident that presence or absence of a perianth-tube is not necessarily a decisive character.

When other features are considered, *Triteleia* is found to show a close resemblance to *Bloomeria crocea*,¹ and it is quite remarkable that the points of resemblance between *Triteleia* and *Bloomeria* correspond almost exactly with the points of difference between *Triteleia* and *Brodiaea*. The corms of *Bloomeria* are almost indistinguishable from those of *Triteleia* but have pale brownish rather than straw-colored coats. The solitary leaf of *Bloomeria crocea* has exactly the same structure as the leaves of *Triteleia*, being keeled on the back and doubly channeled on the upper surface. *Triteleia* always has either one or two leaves from each corm, whereas in *Brodiaea* the leaves from mature corms are never solitary and are frequently as many as five. The teratological compound umbels of *Bloomeria* (observed in cultivated plants) have the same structure as those of *Triteleia*, one of the flowers being replaced by a perianth-like involucre from which pedicels arise.

In flower structure there is also great similarity between *Triteleia* and *Bloomeria*. Both have versatile anthers which are distant from the style, differing from those of *Brodiaea* in both attachment and position. There is a suggestion of homology between the stamens of *Bloomeria crocea*, which are appendaged at the base, and those of *Triteleia ixioides*. In *T. ixioides* the filaments are forked at the apex in a manner suggesting the basal appendages of *Bloomeria*, and between the forks the anther is borne on a short stalk perhaps corresponding to the slender filament of *Bloomeria*. The stigma in the two genera is identical in structure, having three small lobes not spreading beyond the diameter of the style.² The seeds of *Bloomeria*, like those of *Triteleia*, are coarsely pitted, minutely granulate, and ridged on one side.

¹ In certain respects *Bloomeria Clevelandii* more closely resembles *Milla* than the type species of *Bloomeria*. Macbride (1918) has combined *Milla* with *Bloomeria* for reasons that seem logical. However, final conclusions in the classification of this group can be reached only after study of all the species in the living condition, preferably in the field. Because of my lack of field acquaintance with several of these species, the present discussion of the characters of *Bloomeria* is intentionally limited to *B. crocea*.

² The description of the stigma of *Triteleia* as "not evidently lobed" (Hoover, 1939) was inaccurate. During 1939 fresh flowers of most species of the genus were examined, and invariably the stigma showed three lobes, small and inconspicuous but easily visible. In herbarium material these lobes usually can not be seen.

The significant differences between *Triteleia* and *Bloomeria* are apparently only two: the distinct perianth-segments and the sessile ovary of the latter genus. When it is recalled that the length of the perianth-tube and of the stipe of the ovary vary to a great degree in *Triteleia*, even these features lose much of their impressiveness. If the differences between *Triteleia* and *Brodiaea* are compared, the relationship of *Triteleia* to *Bloomeria* seems very close indeed. The presence or absence of a perianth-tube has been given an emphasis apparently out of proportion to its actual significance. The status of *Bloomeria* as a genus appears never to have been questioned, at least by American botanists, since its publication. The conclusion seems inevitable, in view of the observations recorded above, that *Triteleia* is equally distinct both from *Milla* and from *Brodiaea*. Although it is not here suggested that *Bloomeria* be included in *Triteleia*, it is believed that there is truly a close relationship between the two genera, whereas the superficial similarity between certain species of *Triteleia* and *Brodiaea* is more probably the result of parallel development.

While many botanists have combined *Triteleia* with *Brodiaea*, others have divided it into smaller genera. *Hesperoscordum*, of which *T. hyacinthina* is the original species, was published by Lindley (1830) at the same time as *Triteleia*. The two characters which have been used as the basis for separating *Hesperoscordum* are the deltoid-dilated filaments and the bowl-shaped perianth with a short tube. A consideration of certain critical forms indicates that both of these features are taxonomically unimportant. In the rare plant named by Greene *Triteleia lilacina*, here treated as a variety of *T. hyacinthina*, the perianth is bowl-shaped but the filaments are filiform. Furthermore, triangular-dilated filaments occur in *T. Bridgesii*, in *T. clementina*, and apparently even in *T. grandiflora*, the standard species of the genus. In the shape of the perianth, the Arizona species, *T. Lemmonae*, is very similar to *T. hyacinthina* except that the short tube tends to be acute at the base, thus suggesting an approach to such species as *T. peduncularis*. Even in *T. hyacinthina* the perianth becomes pointed at the base in fruit. Because of these facts, there seems to be no adequate reason for regarding *T. hyacinthina* as the type of a distinct genus. Although *Triteleia* and *Hesperoscordum* were published on the same page, *Triteleia* has precedence under the International Rules of Nomenclature of 1905, article 46, since Greene (1886) in combining the two used *Triteleia* as the name for the enlarged genus.

The genus *Calliprora* was based by Lindley (1833) on *C. lutea*, which is now known under the specific name *ixioides*. The structure of the filaments of *T. ixioides*, which are broad and flat and forked at the apex, has constituted the principal basis for the recognition of *Calliprora*. Two rare plants which obviously are closely related to *T. ixioides* are significant in this regard. *Triteleia lugens* Greene is like *T. ixioides* in having the filaments alternately long and short, and resembles that species so closely that many authors have not considered it to be distinct, but the filaments are rounded at the apex like those of *Triteleia Howellii* (Wats.) Greene, a plant universally regarded as closely related to the type species of *Triteleia*. Another species, described as new in this revision, is also very similar to *T. ixioides* except that the filaments are

triangular-acuminate like those of *T. Bridgesii*. There thus remains no adequate reason for recognizing *Calliprora* as a genus. It is of interest in this connection that an apparent hybrid combining the characters of *T. ixioides* and *T. Bridgesii* appeared in my garden, where those two species were cultivated together.

The third proposed segregate genus, *Seubertia*, was based by Kunth (1843) on *Triteleia laxa* and was distinguished principally by having the perianth tube attenuate at the base. However, several species are intermediate in the shape of the perianth between *T. laxa* and *T. grandiflora*, in which the tube is rounded at the base. Because of this fact, very few botanists have attempted to maintain *Seubertia* as a genus. It may therefore be regarded as synonymous with *Triteleia*.

A notable fact which gives support to *Triteleia* as a single genus is the uniformity in the length of the style, which is never less than 2 mm. or more than 4 mm. long, notwithstanding wide variation in the size of the perianth.

The definition of *Triteleia* which is here accepted may be further confirmed by the presence of a peculiar retrorse pubescence on the lower part of the scape in several species, especially in certain forms of *T. hyacinthina*, *T. ixioides*, and *T. laxa*, the three species which have been taken as the types of segregate genera. This sort of pubescence also occurs occasionally in *Bloomeria* but is unknown in any other genus of Alliioideae. It is therefore another indication of the validity of *Triteleia* and of the close relationship between this genus and *Bloomeria*.

Although the preceding discussion indicates that *Triteleia* is one well defined genus, it can still be divided readily into three smaller groups. Certain species have the stamens attached alternately in two rows on the perianth. This group, because it includes the original species of the genus, is to be called section *Eutriteleia*. Among the species with stamens attached at the same level, the group in which the filaments are alternately long and short may be distinguished as section *Calliprora*, while the species with equal stamens are taken to constitute section *Hesperoscordum*.

These groups of species are better regarded as sections than as subgenera because the differences seem rather trivial, and it is even possible that the division of the genus on these grounds may be artificial. In general aspect there is considerable similarity not only between *T. laxa* of *Eutriteleia* and *T. Bridgesii* of *Hesperoscordum*, but also among *T. crocea*, *T. ixioides* var. *analina*, and *T. montana*, representing all three sections. Furthermore, parallel variation within each section can be demonstrated in such features as flower color, shape of perianth, and shape of stamens. Nevertheless, it seems desirable to recognize the three sections for reasons of convenience.

Nearly all species of *Triteleia* reproduce by simple division of the corms, although several of the species include varieties or races in which vegetative reproduction seldom or never occurs. Frequently the division of the corm results in the formation of one or a few small corms and a central large one, but no species of *Triteleia* is known to produce a circle of specialized bulblets

around the base of the corm as do most species of *Brodiaea*. Offsets of a specialized sort are reported by J. P. Tracy (quoted by Jepson, 1922) to occur in *T. peduncularis* but have not been seen by me.

The geographical center of distribution of *Triteleia* is in the "Klamath Area," an important endemism area of southwestern Oregon and northwestern California. Two species, *T. crocea* and *T. Hendersoni*, are restricted to that area, six species of wider distribution also occur there, and the remaining six species of the genus are all of localized distribution in widely separated areas to the south. Like many other genera of western North America, *Triteleia* is represented in the northern part of its range only by species of wide distribution, while toward the south, where climatic diversity presumably has stimulated the production of new forms, are found a number of endemic species. The northern limit of distribution of the genus is marked by the occurrence of the widely distributed *T. grandiflora* in British Columbia. The southern limit is reached by *T. lugens*, a species which appears to be rather widely but very sporadically distributed, on Guadalupe Island off the coast of Baja California. In southern California the genus is quite rare but is represented by an endemic species on San Clemente Island. The eastern limit of distribution of *Triteleia* closely follows parallel 111 of west longitude from Gallatin County, Montana, through western Wyoming to the northern Wasatch Mountains of Utah, where *T. grandiflora* reaches its southeastern limit, and in north central Arizona, where *T. Lemmonae* is endemic. The genus is most fully represented near the Pacific coast, but typical *T. grandiflora* is found only to the east of the Cascade Range, *T. hyacinthina* and a variety of *T. ixioides* are common on the east slope of the Sierra Nevada, and *T. Lemmonae* is far removed from the ocean. The wide distribution in very diverse climatic areas, the great variety of form, and the large number of entities of localized or restricted distribution all indicate that *Triteleia* is of greater antiquity than such genera as *Bloomeria* or *Brodiaea*.

Material for study has been available from the following herbaria: California Academy of Sciences (CA), herbarium of W. L. Jepson (J), Los Angeles Museum (LA), Oregon State College (OS), Pomona College (P), Dudley Herbarium, Stanford University (S), Natural History Museum of San Diego (SD), herbarium of J. William Thompson (T), University of California (UC), University of Oregon (UO), University of Washington (UW), Vegetation Type Map Herbarium, California Forest and Range Experiment Station (VTM), Willamette University (W), and Washington State College (WS). To those in charge of these herbaria I wish to express my sincere thanks. Except for some of the rarest species and varieties, only a small proportion of the collections which were seen are cited. The principal object in the selection of specimens for citation has been to give an accurate indication of geographical distribution.

To all who have assisted in the preparation of this revision by supplying me with plants, offering suggestions, or otherwise, I am very grateful. Because of my lack of opportunity for field study of several of the species, the help of these friends has been of great value.

TRITELEIA Dougl. ex. Lindl., Bot. Reg. 15: under pl. 1293. 1830, emend. Greene, Bull. Cal. Acad. 2:138. 1886.

Brodiaea subgenus *Triteleia* Eastwood, Bergen's Elements of Botany, Pacific Coast Edition, Key and Flora 21. 1897. *Hesperoscordum* Lindl., Bot. Reg. 15: under pl. 1293. 1830. *Brodiaea* subgenus *Hesperoscordum* Eastwood, l. c. *Calliprora* Lindl., Bot. Reg. 19: pl. 1590. 1833. *Brodiaea* section *Calliprora* Wats., Proc. Am. Acad. 14: 238. 1879. *Brodiaea* subgenus *Calliprora* Eastwood, l. c. *Seubertia* Kunth, Enum. Pl. 4: 475. 1843. *Brodiaea* section *Seubertia* Wats., Proc. Am. Acad. 14: 237. 1879.

Perennial herbs with scapes and leaves arising directly from a corm. Corm with reticulate-fibrous straw-colored coats. Leaves one or two from each corm, narrowly linear and much elongated, flattened, keeled on the lower side, with two parallel channels on the upper side. Scape rather slender (1 to 5 mm. in diameter), smooth, retrorsely scabrous, or hairy toward the base. Inflorescence umbellate, subtended by an involucre of distinct bracts. Involucral bracts scarious or green (in *T. Lemmonae* often purplish), acuminate. Pedicels jointed to the flowers. Perianth of six segments joined below to form a tube of varying length and shape. Stamens six, all fertile, the anthers all alike, versatile, the filaments distinct, either all alike, of unequal length, or unequally inserted. Style continuous with the ovary, slender, 2 to 4 mm. long in all species, three-lobed in cross section, each lobe terminating in a lobe of the small stigma. Ovary and capsule stipitate, loculicidal. Seeds black, rounded, ridged on one side, coarsely and irregularly pitted, minutely granulate or granulate-reticulate.

Type species: *Triteleia grandiflora* Lindl.

KEY TO THE SPECIES

- Stamens attached alternately at two different levels, thus forming two rows....*Eutriteleia*.
 Perianth-tube obtuse and rounded at base1. *T. grandiflora*.
 Perianth-tube acute or attenuate at base.
 Pedicels 2 to 5 times as long as flowers, rarely less; perianth-tube acute at base, not attenuate.
 Filaments unequal, those of lower row shorter; anthers 2 to 4 mm. long; seeds about 2 mm. long.2. *T. peduncularis*.
 Filaments equal; anthers 1.5 mm. long; seeds 3 to 4 mm. long. 3. *T. clementina*.
 Pedicels often shorter than flowers, very rarely more than twice as long; perianth-tube attenuate at base.
 Perianth 18 to 47 mm. long, blue or sometimes white; filaments nearly equal.4. *T. laxa*.
 Perianth 14 to 19 mm. long, usually yellow, rarely blue; filaments of lower row of stamens very short.5. *T. crocea*.
 Stamens all attached at the same level at mouth of perianth-tube.
 Stamens alternately long and short.*Calliprora*.
 Filaments not forked at apex.
 Perianth-tube equalling the segments; filaments attenuate upward....6. *T. Dudleyi*.
 Perianth-tube much shorter than the segments; filaments with broad rounded apex.7. *T. lugens*.
 Filaments forked at apex.
 Perianth-segments abruptly spreading, forming an angle at the mouth of the tube; longer stamens 1/3 to 1/2 as long as perianth-segments; forks of at least the longer filaments divergent.8. *T. ixioides*.
 Perianth open-campanulate at anthesis, the segments not forming an angle with the tube; longer stamens 2/3 as long as perianth-segments; forks of filaments not divergent.9. *T. versicolor*.

- Stamens equal or nearly so. *Hesperoscordum*.
 Perianth 9 to 23 mm. long, bowl-shaped or the tube moderately attenuate, the segments at least twice as long as the tube.
 Perianth spreading from the base, not at all attenuate at anthesis, the segments two to three times as long as the tube.
 Perianth white, blue, or lilac; filaments triangular-dilated, or in the variety slender and not dilated. 10. *T. hyacinthina*.
 Perianth "deep orange"; filaments stout, hardly dilated. 11. *T. Lemmonae*.
 Perianth funnelliform, attenuate at base, the segments about twice as long as the tube.
 Perianth 12 to 15 mm. long; stamens about two-thirds as long as perianth-segments. 12. *T. montana*.
 Perianth 19 to 23 mm. long; stamens less than half as long as perianth-segments. 13. *T. Hendersoni*.
 Perianth 27 to 45 mm. long, with strongly attenuate tube longer than the segments. 14. *T. Bridgesii*.

Section 1. TRITELEIA section *Eutriteleia* nom. nov.

Triteleia Dougl. ex Lindl., Bot. Reg. 15: under pl. 1293. 1830, excluding *T. bivalvis* and *T. uniflora*.

1. *Triteleia grandiflora* Lindl., Bot. Reg. 15: under pl. 1293. 1830.

Milla grandiflora Baker, Trans. Linn. Soc. 11: 380. 1871. *Hookera grandiflora* Ktze., Rev. Gen. Pl. 1: 712. 1891. *Brodiaea grandiflora* Macbr., Contr. Gray Herb. 56: 9. 1918; not *B. grandiflora* Smith. *Brodiaea Douglasii* Wats., Proc. Am. Acad. 14: 237. 1879. *Hookera Douglasii* Piper, Contr. U. S. Nat. Herb. 11: 190. 1906.

Leaves 4 to 10 mm. wide; scape 2 to 7 dm. tall; pedicels ascending, 1 to 4 cm. long, mostly shorter than the flowers at anthesis, in fruit mostly a little longer; perianth usually bright blue, occasionally varying to white, the tube rounded at base, 8 to 18 mm. long, the segments apparently spreading at anthesis, 9 to 13 mm. long; stamens alternating in two rows; filaments of upper row of stamens about 2 mm. long, slender but somewhat dilated toward the base, those of the lower row less than 1 mm. long; anthers 2 to 3 mm. long; stipe of ovary about half as long as the body.

Eastern British Columbia to eastern Oregon and northern Utah, east of the Cascade Range.

BRITISH COLUMBIA: Mainland: Lake Osoyoos, 1905, *Macoun* (P); west of Cascade, 1902, *Macoun* (P). WASHINGTON: Okanogan Co.: Ross Canyon, *Fifer* 50 (WS); Brewster, 1934, *MacFarlane* (UW). Ferry Co.: Curlew, *Sprague* 128 (WS); 8 miles northeast of Republic, *Spiegelberg* 80 (WS). Stevens Co.: 6 miles east of Colville, *Sprague* 136 (WS); Chelewah, *Sprague* 121 (WS). Pend Oreille Co.: Locke, *Spiegelberg* 78 (WS). Chelan Co.: 10 miles north of Entiat, *Thompson* 6016 (OS, S, T); north of Wenatchee, *Benson* 1300 (S, UW). Spokane Co.: Hangman Creek, *Sandberg* and *Leiberg* 71 (CA, UC, UO, WS); Williams Lake, 1926, *Whicker* (WS). Grant Co.: near Coulee City, *Thompson* 6114 (OS, S, T). Kittitas Co.: Ellensburg, 1896, *Piper* (WS); Ginkgo State Park, *H. W. Smith* 394 (UW). Adams Co.: Washucna, *Cotton* 986 (WS); Palouse Falls, *Constance* and *Rollins* 1506 (WS). Whitman Co.: Almota Canyon, *Constance*, *Machlis*, *Rogers*, and *Rollins* 1047 (CA, S, UC, UW, WS); Wawawai, *St. John* 5958 (S, WS). Franklin Co.: Kahlotus, *Cotton* 1015 (WS); Pasco, 1896, *Hinshaw* (UW). Columbia Co.: Stockade Springs, *St. John* and *Smith* 8294 (WS); 4 miles north of Table Rock, *Constance*, *Clarke*, *Staats*, and *Van Fleet* 1276 (WS). Garfield Co.: near Clearwater Ranger

Station, Constance and Clements 1740 (WS). Asotin Co.: near Silcott, Applegate 6762 (S); 1 mile west of Anatone, 1933, Sprague (OS, S). Klickitat Co.: Carley to Roosevelt, Pickett, McMurray, and Dillon 1417 (WS). OREGON: Umatilla Co.: Umatilla, 1882, T. Howell (OS, S, UO); 10 miles east of Pendleton, Sherwood 328 (W). Wallowa Co.: Snake River Canyon near mouth of Battle Creek, Peck 18146 (S, W); 5 miles west of Imnaha, Sherwood 231 (W). Union Co.: 6 miles west of Summerville, 1933, Sprague (OS, S). Baker Co.: near Baker, Hanna 1668 (UW); Huntington, Holway 48 (UO). Grant Co.: Squaw Creek near Humphrey Ranch, Henderson 5115 (CA, S, UO); Strawberry Peak, Applegate 6208 (S, UC). Crook Co.: Ochoco Ranger Station, Peck 17023 (W); 5 miles west of Prineville, Peck 15968 (W). Harney Co.: Silvies River, Peck 1353 (W); hills of South Malheur River 8 miles from Crane, Henderson 8826 (CA, UO). Malheur Co.: Brogan, 1910, Cooper (W). Lake Co.: near Alkali, 1888, B. Anderson (OS). IDAHO: Kootenai Co.: south end of Lake Pend Oreille, 1891, Leiberg (UO); Albany Falls, Sprague 108 (WS). Latah Co.: above Camp Cougar, Thatuna Hills, Dillon 578 (WS); Moscow, Abrams 596 (S, UC). Nez Perce Co.: Lewiston, Heller 2971 (S, UC); Hatwai Creek, Sandberg, MacDougal, and Heller 30 (CA, P, S). Lewis Co.: Winchester, 1929, Phelps (CA). Idaho Co.: Meadow Creek above Selway Falls, Constance and Rollins 1635 (WS); 2 miles north of Sheep Creek, Snake River Canyon, Constance, Rollins, and Dillon 1599 (WS). Valley Co.: South Fork Ranger Station, Bolles 14 (OS). Washington Co.: Deer Lake, 1899, M. E. Jones (P); Weiser, 1900, M. E. Jones (P). Gem Co.: Squaw Creek (Sweet), Macbride 814 (P, S, UC, WS). Ada Co.: Boise, Clark 39 (P, S, UC). Fremont Co.: Targhee Pass, Applegate 6357 (S); Henry Lake, Payson 1941 (CA). MONTANA: Flathead Co.: Big Fork, 1908, M. E. Jones (P). Lake Co.: Wild Horse Island, 1908, M. E. Jones (P). Missoula Co.: Evaro, 1909, M. E. Jones (P); Missoula, 1890, Wright (UC); Mt. Sentinel, Hitchcock 1612 (P). Ravalli Co.: Alta, 1909, M. E. Jones (P). Gallatin Co.: Belgrade, 1901, Moore (S, UC); Meadow Creek road, 1933, Swingle (UW). WYOMING: Teton Co.: Canyon Creek, Williams 798 (CA). UTAH: Cache Co.: Logan Canyon, 1930, Van Dyke (CA). Davis Co.: Farmington, M. E. Jones 2156 (P); East Bountiful, 1908, Clemens (S). Salt Lake Co.: City Creek Canyon, 1895, Snyder (S). Summit Co.: Parley's Canyon, 1901, Stokes (S, UC), 1920, Hapeman (S). Wasatch Co.: Midway, Eastwood and Howell 512 (CA).

This species, the type of the genus, is unique in the shape of the perianth, but in all characters of generic value in this group, including the structure of the stigma and the seeds, it corresponds with the other species referred to *Triteleia*. Next to *T. hyacinthina*, *T. grandiflora* is the most widely distributed species of the genus, evidently being common throughout the region between the Cascade Range and the northern Rocky Mountains. The localities in Gallatin County, Montana, mark the eastern limit of distribution of the genus and its only known occurrence east of the Continental Divide. Typical *T. grandiflora* is remarkably uniform throughout most of its range, but toward the west, where the following variety and intergrading forms occur, there is some variation in certain details of flower structure.

1a. *Triteleia grandiflora* Lindl. var. **Howellii** (Wats.) comb. nov.

Brodiaea Howellii Wats., Proc. Am. Acad. 14: 301. 1879. *T. Howellii* Greene, Bull. Cal. Acad. 2: 139. 1886. *Hookera Howellii* Piper, Contr. U. S. Nat. Herb. 11: 190. 1906. *Brodiaea bicolor* Suksd., West. Am. Sci. 14: 1. 1902. *Hookera bicolor* Piper, Contr. U. S. Nat. Herb. 11: 190. 1906. *T. bicolor* Heller, Muhl. 6: 83. 1910.

Filaments (of both rows) broad, rounded at apex; stamens sometimes

larger, the anthers as much as 4 mm. long and the filaments correspondingly long.

Southern part of Vancouver Island, British Columbia, to extreme northern California (Siskiyou County), mostly west of the Cascade Range but extending into the Columbia River valley and the Klamath Lake region.

BRITISH COLUMBIA: Vancouver Island: Thetis Lake, 1904, *Anderson* (WS), 1912, *Anderson* (WS), 1914, *Henry* (CA); Victoria, *Henry* 1201 (CA). WASHINGTON: Island Co.: Goose Rock, *H. W. Smith* 920 (UW), *G. N. Jones* 4841 (UW), 6146 (UW); Whidby Island, *Gardner* 285 (UW, WS). Grant Co.: near Ephrata, *Thompson* 6119 (T). Kittitas Co.: north of Ellensburg, *Thompson* 6218 (OS, S, T). Pierce Co.: Tacoma, 1906, *Flett* (WS). Thurston Co.: Bush Prairie, 1906, *Townsend* (WS). Yakima Co.: North Yakima, *Henderson* 2406 (WS); Medicine Valley, *Heidenreich* 76 (WS). Skamania Co.: near Rands, *Hitchcock and Marsh* 3303 (CA, UC); Underwood, *Beattie* 3809 (WS). Klickitat Co.: near Bingen, *Suksdorf* 4448 (S, UO), *Thompson* 11531 (P, S, T, UW); near Maryhill, *Thompson* 8181 (CA, T, UC); Falcon Valley, *Suksdorf* 2491 (S, UC). OREGON: Gilliam Co.: Rock Creek, 1926, *Bellinger* (W). Sherman Co.: near mouth of John Day River, *Henderson* 5114 (CA, S, UO). Wasco Co.: 5 miles west of The Dalles, *Thompson* 4215 (S, T); 10 miles north of Wapinitia, *Peck* 17392 (S, W). Hood River Co.: Hood River, *Henderson* 964 (OS), *Peck* 14834 (S, W). Multnomah Co.: Bridal Veil, *Drake and Gorman* 399 (UO). Clackamas Co.: south slope of Mt. Hood, 1933, *Peck* (W); Barlow's Gate, 1881, *T. Howell* (OS, WS). Yamhill Co.: 2 miles north of Amity, *Peck* 14804 (W); near Amity, *Thompson* 2493 (S, T). Benton Co.: Corvallis, *Stason* 2308 (UC). Linn Co.: Brownsville, *Haskin* 4 (S), 128 (UO). Lane Co.: Old Baldy, Coburg Hills, 1925, *Constance* (UC); Spencer Creek district west of Eugene, 1937, *Sipe* (UO). Klamath Co.: Four Mile Creek, near Pelican Bay, *Applegate* 4697 (S); 15 miles southwest of Lake of the Woods, *Peck* 16703 (W). Jackson Co.: Pinehurst, *Applegate* 4281 (S). CALIFORNIA: Siskiyou Co.: Hornbrock, 1890, *Howell* (UO).

Although well defined geographically, this form differs from typical *T. grandiflora* only in the shape of the filaments. Several specimens from the part of the Columbia River valley where both forms occur appear to represent intergrades between the two. For that reason it seems inadvisable to maintain *T. Howellii* as a species. Large anthers are found only in the variety, but usually the anthers are no larger than in typical *T. grandiflora*. *Brodiaea bicolor* Suksd. is merely a color form having a perianth with blue tube and white segments. The difference in relative length of perianth-tube and segments first used as a key character by Piper (1911) and later by Abrams (1923) is not consistent and does not make it possible to divide a series of specimens into two distinct groups. The types of both *B. Howellii* Wats. and *B. bicolor* Suksd. were collected in Klickitat County, Washington. Both in typical *T. grandiflora* and in var. *Howellii* the flowers vary from bright blue to white, but bicolored flowers apparently occur only in plants with broad filaments.

From herbarium records, var. *Howellii* seems to be common in the Columbia River region but of rather rare occurrence elsewhere.

2. *Triteleia peduncularis* Lindl., Bot. Reg. 20: under pl. 1685. 1835.

Milla peduncularis Baker, Journ. Linn. Soc. 11: 384. 1871. *Brodiaea peduncularis* Wats., Proc. Am. Acad. 14: 237. 1879. *Hookera peduncularis* Ktze., Rev. Gen. Pl. 1: 712. 1891.

Corm shallowly seated, freely dividing; leaves 5 to 15 mm. wide; scape 1 to 4 dm. tall, smooth; pedicels ascending, 2 to 18 cm. long; perianth broadly funnelform-campanulate, 15 to 28 mm. long, white or tinged with lilac, in drying frequently becoming lilac or bluish, the segments not abruptly spreading; filaments narrowly subulate, those of the upper row of stamens 2 to 3 mm. long, those of the lower row 1 to 1.5 mm. long; anthers white, 2 to 4 mm. long; ovary yellow, the body about equalling the stipe at anthesis, longer in fruit.

Coast Ranges of California from Humboldt and Tehama Counties to Monterey County.

CALIFORNIA: Humboldt Co.: Eureka, *Tracy* 1920 (P, UC). Tehama Co.: Mud Flat, *Heller* 11528 (CA, OS, S, UC). Mendocino Co.: "north road" to Glen Blair, *Eastwood* and *Howell* 6222 (CA); hills near Covelo, *Eastwood* 15184 (CA); Sherwood Valley, 1899, *Dudley* (S); 6 miles west of Ukiah on Low Gap Road, *Abrams* 8144 (S). Lake Co.: Indian Valley, 1882, *Cleveland* (SD, UC); between Hough's Springs and Colusa County line, *Heller* 12382 (CA, OS, S); Allen Springs, 1882, *Cleveland* (S, SD); Whispering Pines Resort, *M. S. Baker* 2245b (UC); Oak Park Springs, *Bacigalupi*, *Ferris*, and *Wiggins* 6691 (S, UC). Napa Co.: south fork of Butts Creek, *Hoover* 3541 (CA, UC); head of Moore's Creek, *Tracy* 2213 (UC, UO). Sonoma Co.: Pitkin Marsh, *J. T. Howell* 13037 (CA); near Kenwood, *J. T. Howell* 12606 (CA, P); Bodega, *Chandler* 676 (UC). Marin Co.: Point Reyes, *Elmer* 4988 (CA, P, S, UC); Mt. Tamalpais, 1919, *Campbell* (CA, P); Tiburon, *J. T. Howell* 13090 (CA), *Walker* 1725 (UC). Stanislaus Co.: La Puerta Creek, *Elmer* 4348 (CA, OS, P, S, UO, WS). Monterey Co.: Pacific Grove, 1907, *Patterson* and *Wiltz* (S); Patrick Cabin, Carmel River, 1907, *Clemens* (CA).

Triteleia peduncularis flowers in May and June and is always found in places which are wet during the growing season. Although of rather wide distribution in the California Coast Ranges, it is not generally common, and is quite rare south of San Francisco Bay.

The yellow ovary, contrasting with the white perianth, is a notable feature as seen in living plants. In most other species of the genus the ovary is either green or colored like the perianth. The ascending pedicels, which are often very long, also give to this species a distinctive aspect. The *Patterson* and *Wiltz* collection from Monterey County is unusual in having pedicels less than twice as long as the flowers, but is matched in this respect by some of the specimens from Marin County and in all other respects is typical. Plants from Sonoma County have unusually small anthers, sometimes hardly 2 mm. long, but are not distinguishable otherwise.

3. *Triteleia clementina* sp. nov.

Scapo 3 ad 4 dm. alto; pedicellis 3 ad 8 cm. longis; perianthio azureo, 17 ad 25 mm. longo, tubo basi acuto, non attenuato; staminibus et stylo e tubo perianthii vix exsertis; filamentis biseriatis, ad basin dilatatis, 2 mm. longis; antheris ovalibus, 1.5 mm. longis; stipite ovarii in anthesi circa corpore aequilongo, in fructo saepe breviori; seminibus 3 ad 4 mm. longis.

Leaves 4 to 10 mm. wide; scape smooth, 3 to 4 dm. tall; pedicels 3 to 8 cm. long; perianth light blue, 17 to 25 mm. long; the tube acute at base, not at all attenuate; stamens and style hardly exserted from perianth-tube; filaments

alternating in two rows, triangular-dilated toward base, 2 mm. long; anthers oval, 1.5 mm. long; ovary with stipe about as long as the body at anthesis, the body often longer than the stipe in fruit; seeds 3 to 4 mm. long.

Restricted to San Clemente Island, off the coast of southern California.

CALIFORNIA: Los Angeles Co.: San Clemente Island, 1918, Evermann (CA); east side of San Clemente Island in shady, cool canyons, Murbarger 79 (UC, type); canyon running from Lemon Tank, Munz 6695 (P).

This very rare plant is evidently the only species of *Triteleia* occurring on any of the islands off the southern California coast. It is remarkably similar morphologically, particularly in the length of the pedicels and the size and shape of the flowers, to *T. peduncularis*, a species geographically remote. The early flowering season (March) and blue flowers of *T. clementina*, however, show it to be distinct, and the resemblance to *T. peduncularis* is probably the result of parallel development. For geographical and ecological reasons, the nearest relationship of *T. clementina* appears to be with *T. laxa*, which it closely resembles in general aspect, rather than with *T. peduncularis*. *Triteleia clementina* is like *T. laxa* in having the filaments of the two rows of stamens equal, but differs in its long pedicels (in proportion to the length of the flowers), lack of slender basal portion of the perianth-tube, short dilated filaments, small anthers, and short stipe of the ovary. In addition, the seeds are notably larger than any observed in *T. laxa*.

4. *Triteleia laxa* Benth., Trans. Hort. Soc. ser. 2, 1:143. 1835.

Scubertia laxa Kunth, Enum. Pl. 4: 475. 1843. *Milla laxa* Baker, Journ. Linn. Soc. 11: 384. 1871. *Brodiaea laxa* Wats., Proc. Am. Acad. 14: 237. 1879. *Hooberia laxa* Ktze., Rev. Gen. Pl. 1: 712. 1891. *T. candida* Greene, Bull. Cal. Acad. 2: 139. 1886. *Brodiaea candida* Baker, Gard. Chron. ser. 3, 20: 239. 1896. *B. laxa* var. *candida* Jepson, Fl. Cal. 1: 284. 1922. (?) *Scubertia obscura* Borzi, Boll. R. Ort. Bot. Palermo 1: 18. 1897 (referred to this species by compiler of Index Kewensis). *T. angustiflora* Heller, Bull. S. Cal. Acad. 2: 66. 1903. *Brodiaea laxa* var. *nimia* Jepson, Man. Fl. Pl. Cal. 225. 1923. *B. laxa* var. *Tracyi* Jepson, l. c.

Leaves 4 to 25 mm. wide; scape 1 to 7 dm. tall, smooth or sometimes scabrous or hairy near the base; pedicels 1 to 9 cm. long, ascending or spreading, usually somewhat bent at apex; flowers tending to be horizontal, with the pistil along the lower side and the filaments curved upward; perianth blue or rarely white, 18 to 47 mm. long, the tube attenuate at base, the segments gradually spreading; interior of perianth-tube with six narrow longitudinal membranous appendages near base arising from the adnate portion of the filaments; stamens alternating in two rows, the filaments of both rows 3 to 6 mm. long, filiform; anthers 2 to 5 mm. long; stipe of ovary about 2 to 3 times as long as the body at anthesis, often shorter than the body in fruit.

Extreme southwestern Oregon (Curry County) to Los Angeles County, California.

OREGON: Curry Co.: Harbor, Peck 1352 (W). CALIFORNIA: Del Norte Co.: Wilson Creek between Requa and Crescent City, Abrams and Bacigalupi 8319 (P, S); 3 miles northwest of Requa, 1921, McGregor (S). Humboldt Co.: Big Lagoon, Jepson 9412a (J, type of *Brodiaea laxa* var. *Tracyi* Jepson); Eureka, Tracy 3013

(UC), 3711 (UC); Miranda, Kildale 2005 (S). Shasta Co.: near Redding, Tebbe 56 (UC). Tehama Co.: Red Bluff, 1915, L. E. Smith (CA); Paskenta, Jepson 16316 (J). Mendocino Co.: near Red Mt., Eastwood and Howell 4625 (CA); Fort Bragg, Eastwood 1625 (CA). Butte Co.: 8 miles north of Oroville, Heller 11265 (CA, OS, S, UC); Feather River above Oroville, Heller 10708 (S, UC). Glenn Co.: Alder Springs, Heller 12750 (CA, OS, S). Colusa Co.: Williams, Benson 1044 (UW); 5 miles west of Arbuckle, Ferris 599 (S). Lake Co.: Mt. Sanhedrin, Hall 9466 (UC); ridge west of Leesville, Heller 13133 (CA, S); Oak Park Springs, Bacigalupi, Ferris, and Wiggins 6692 (S, UC). Sutter Co.: 4 miles northeast of Sutter, Embree 32 (VTM); slopes of West Butte, Ferris 6352 (P, S). Yolo Co.: near Winters, Eastwood 14232 (CA). Sacramento Co.: 1/4 miles southeast of Orangevale, Carter 1247 (CA, UC, WS); Elk Grove, 1882, Drew (UC). Solano Co.: near Vacaville, Heller and Brown 5405 (S); near Fairfield, Heller and Brown 5372 (S). Napa Co.: Pope Valley, 1931, Jussel (CA); White Sulphur Spring, Chandler 7564 (UC). Sonoma Co.: Stewart's Point, Abrams 7636 (S); Santa Rosa Creek Canyon, M. S. Baker 580 (UC). Marin Co.: Point Reyes, Eastwood 4755 (CA); Tiburon peninsula, Heller 5728 (P, S, isotypes of *T. angustiflora* Heller). Contra Costa Co.: 3 miles south of Antioch, Heller 8902 (S); Oakland Hills, J. T. Howell 6468 (CA, P, S). Alameda Co.: Berkeley, Walker 148 (UC); Arroyo Mocho, J. T. Howell 811 (CA). San Francisco Co.: Laurel Hill Cemetery, Eastwood 228 (CA). San Mateo Co.: Belmont, Keck 1466 (OS, UW); La Honda, 1925, U. S. Grant (SD). Santa Clara Co.: Stanford University, Elmer 5044 (CA, OS, P, S, UC, UO, WS); San Antonio Valley, Elmer 4329 (CA, P, S, UC, UO); foothills west of Los Gatos, Heller 7389 (OS, S, UC). Santa Cruz Co.: near Bolsa Point, Akey 26 (VTM); mouth of Finny Creek, Wilson 236 (VTM). San Benito Co.: Emmet to Panoche Pass, Abrams and Borthwick 7914 (S); Griswold Creek, Abrams and Borthwick 7948 (S). Eldorado Co.: Coloma, 1928, Vortiede (CA). Amador Co.: Caminetti Ranch near Jackson, Mulliken 112 (P, S, UC); Pine Grove, Hansen 39 (S). Calaveras Co.: Mokelumne Hill, 1895, Blaisdell (CA); 2 miles northeast of Wheat, Johannsen 861 (VTM). San Joaquin Co.: near Stockton, Stanford 192 (OS); Tracy, 1899, Cobb (UC). Tuolumne Co.: near French Flat, Ferris 1581 (CA, P, S); near Peoria Pass, Ferris 1597 (CA, S). Stanislaus Co.: Modesto, Hoover 368 (CA, UC); 3 miles west of Patterson, Schreiber 2372 (VTM). Mariposa Co.: White Rock, 1892, Congdon (S). Merced Co.: Yosemite Road at county line, Schlobohm 63 (VTM); 3 miles southwest of Gustine, Hoover 4236 (UC). Fresno Co.: Piedra, Hoover 3983 (CA, S, UC). Tulare Co.: Lindsay, 1928, Harter (CA); Porterville, 1922, Kelley (CA). Kern Co.: near Glenville, J. T. Howell 5112 (CA, P); Hobo Hot Springs, Abrams 11948 (P, S); Water Canyon, Abrams and McGregor 435 (S). Santa Barbara Co.: San Miguelito Canyon, Munz 10256 (P). Los Angeles Co.: Hollywood, Davidson (LA).

Triteleia laxa is very common at low altitudes in central California. It grows under various ecologic conditions, with wide attendant variation, especially in flower size. A form with very large flowers, frequently over 4 cm. long, occurs in the southern Sierra Nevada foothills and on the east side of the San Joaquin Valley. The leaves also are often extremely large in such plants. *Triteleia candida* Greene, based on a specimen from the foothills east of Fresno, probably is referable to that form, but the flowers were described at white. I could find no plants with white flowers in the type region of *T. candida*, but such plants might be expected to occur anywhere within the range of the species. Strangely enough, this large-flowered form has anthers only 2 to 3 mm. long. There is, however, so much variability in anther size both near the coast and in the interior of California that it is impractical to segregate a variety on that basis. For example, Heller 7389, collected in Santa Clara County, has smaller anthers than most specimens from the Sacramento Valley.

The plants with larger anthers and flowers of average size, which occur nearly throughout the range of the species, show a few notable minor variations. A form with scapes retrorsely hairy near the base is common on the east side of the Sacramento Valley but of very rare occurrence elsewhere. Plants of the Sacramento Valley ordinarily have flowers of the same sky-blue color as the large-flowered form previously mentioned and, like it, flower mainly in March and April. The flowers of the coastal form, which appear mostly in May and June, are usually very deep blue. It has also been observed that the corms of the coastal form divide more freely. White-flowered plants have been collected at various localities but are most plentiful in the foothills on the west side of the lower San Joaquin Valley. The northern coast form which has been called *Brodiaea laxa* var. *Tracyi* Jepson is remarkable for its late flowering season (August) but seems to be quite identical morphologically with typical *T. laxa*.

Plants with unusually small flowers, sometimes only 18 mm. long, are found in the Coast Ranges of central California associated with the common coastal form of the species. The extreme expression of this variation has been called *Brodiaea laxa* var. *nimia* Jepson, while *Triteleia angustiflora* Heller represents an intermediate state. Such plants grow usually if not always with larger-flowered plants, intergrade completely, and are frequently mixed with them in collections. Occasionally plants of the coastal region may have flowers as large as those of San Joaquin Valley plants. It therefore seems inadvisable to distinguish a variety on the basis of flower size, although the variation is quite impressive. Notwithstanding the variability of the species, *T. laxa* is sufficiently constant in essential characters to be regarded as a single taxonomic unit.

5. *Triteleia crocea* (Wood) Greene, Bull. Cal. Acad. 2:141. 1886.

Seubertia crocea Wood, Proc. Phil. Acad. 1868: 172. 1868. *Milla crocea* Baker, Journ. Linn. Soc. 11: 384. 1871. *Brodiaea crocea* Wats., Proc. Am. Acad. 14: 238. 1879. *Hookera crocea* Ktze., Rev. Gen. Pl. 1: 712. 1891.

Leaves about equalling the scape, 4 to 10 mm. wide; scape 1 to 3 dm. tall, smooth or slightly scabrous near base; pedicels spreading, especially in fruit, and showing a tendency to curve upward, 7 to 20 mm. long; perianth bright yellow, the tube attenuate at base, 5 to 8 mm. long, the segments somewhat ascending, 9 to 11 mm. long; filaments slender, very slightly dilated toward base, those of the upper row of stamens 3 mm. long, those of the lower row 1.5 mm. long; anthers 1.5 to 2 mm. long; stipe of ovary about equalling the body or a little longer.

Josephine and Jackson Counties, Oregon, to Trinity County, California.

OREGON: Josephine Co.: Applegate Bridge, *Gale* 252 (T); between Grants Pass and Selma, 1926, *Gale* (T); Low Gap Trail to Whiskey Peak, *Peck* 16452 (W). Jackson Co.: Ashland (Siskiyou) Peak, 1930, *P. Hitchcock* (UO). CALIFORNIA: Siskiyou Co.: Humbug Mountain, *Butler* 786 (P, S, UC), 1287 (P, S, UC); Yreka, *L. E. Smith* 702 (CA); near Yreka on Fort Jones road, *Eastwood and Howell* 1741 (CA); Shackleford Canyon, *Chandler* 1695 (UC); Mill Creek near Etna Mills, *Kildale* 9831 (S). Shasta Co.: Castella, 1916, *Rosenbaum* (UC). Trinity Co.: 3 miles north of Carrville, 1936, *Cantelow* (CA); Oregon Gulch Mountain, *Tracy* 7539 (UC); Mt. Bally, 1889, *Kleeberger* (CA).

Thiteleia crocea, a species of restricted range, is well characterized and quite uniform morphologically. It was originally based on a collection made at Yreka, California, by Wood. Its flowering season is in May and June.

5a. *Triteleia crocea* (Wood) Greene var. *modesta* (Hall) comb. nov.

Brodiaea modesta Hall, Univ. Calif. Publ. Bot. 6:166. 1915. *T. modesta* Abrams, Ill. Fl. Pac. St. 1:403. 1923.

Flowers blue; plant somewhat smaller throughout.

Local in or near the northern Trinity Mountains of Siskiyou, Shasta, and Trinity Counties, California.

CALIFORNIA: Siskiyou Co.: Castle Lake, July 27, 1911, Condit (UC, type). Shasta Co.: trail to Castle Crag, 1893, Dudley (S). Trinity Co.: 8 miles north of Carrville, 1936, Cantelow (CA).

As has been stated previously by Jepson (1922), there is no morphological difference whatever between this blue-flowered plant and *T. crocea*. There is a tendency in var. *modesta* for all parts of the flower to be smaller and the plant smaller generally, but this difference is slight and not well defined. The blue color form may be recognized as a variety because of its striking appearance and extremely narrow range (even when compared with the restricted range of typical *T. crocea*), and especially because a parallel variant of *T. Hendersoni*, *Brodiaea Leachiae* Peck, seems on account of its geographical isolation to be even more deserving of taxonomic recognition.

Section 2. TRITELEIA section *Calliprora* (Lindl.) comb. nov.

Calliprora Lindl., Bot. Reg. 19: pl. 1590. 1833.

6. *Triteleia Dudleyi* sp. nov.

Cormo profunde posito; foliis 4 ad 8 mm. latis, scapum superantibus vel eo aequilongis; scapo 1 ad 3 dm. alto, laeve; pedicellis gracilibus, ascendentibus, 15 ad 35 mm. longis; perianthio pallide luteo (in sicco purpurascente), tubo 8 ad 12 mm. longo, segmentis lanceolatis, 10 ad 12 mm. longis; filamentis anguste triangularibus, acuminatis, uniserialis, longis et brevibus alternantibus. longioribus circa 3.5 mm. longis, brevioribus circa 2 mm. longis; antheris ovalibus, 1 mm. longis, lavendulaceis; stipite ovarii in anthesi corpore aequilongo.

Corm deep-seated; leaves 4 to 8 mm. wide, surpassing or about equalling the scape; scape 1 to 3 dm. tall, smooth; bracts lanceolate-acuminate; umbel with 3 to 25 flowers; pedicels slender, ascending, 15 to 35 mm. long; perianth "pale yellow" (purplish in drying), the tube slender-funnelform, 8 to 12 mm. long, the segments apparently subrotate, lanceolate, 10 to 12 mm. long; filaments narrowly triangular, acuminate, inserted at the same level, alternately long and short, the longer about 3.5 mm. long, the shorter about 2 mm. long; anthers oval, 1 mm. long, "lavender;" stipe of ovary at anthesis about equalling the body.

Upper Tule River region in the Sierra Nevada of Tulare County, California.

CALIFORNIA: Tulare Co.: Dennison's Trail, alt. 9500 feet, region of upper Tule River, vicinity of Mountain Lake, July 30, 1895, *Dudley* 932 (S. type); black soil, alt. 9500-10500 feet, region of Tule—Little Kern divide, vicinity of Camp Alta, July 31, 1895, *Dudley* 932a (S).

This evidently very rare species has unequal stamens attached at the mouth of the perianth-tube and therefore apparently belongs to the *Calliprora* group. In the form of the stamens, however, it is very different from *T. ixioides*. There is also a less impressive but apparently constant difference between *T. Dudleyi* and all forms of *T. ixioides* in the length of the perianth-tube. The color of the fresh flowers was noted by the collector.

7. *Triteleia lugens* Greene, Bull. Cal. Acad. 2:142. 1886.

Calliprora lugens Greene, Man. Reg. S. F. Bay 319. 1894. *Brodiaea lugens* Baker, Gard. Chron. ser. 3, 20: 459. 1896. *Hookera ixioides* (Ait. f.) Ktze. var. *lugens* Jepson, Fl. W. Mid. Cal. 117. 1901. *Brodiaea ixioides* (Ait. f.) Wats. var. *lugens* Jepson, Fl. W. Mid. Cal. ed. 2, 101. 1911. *Calliprora ixioides* *lugens* Abrams, Ill. Fl. Pac. St. 1: 399. 1923.

Leaves 3 to 10 mm. wide; scape 1 to 4 dm. tall, smooth or slightly scabrous; pedicels 1 to 2.5 cm. long; perianth dull yellow, the tube funnellform, 4 to 5 mm. long, the segments spreading, 8 to 9 mm. long, each with a dark mid-vein; stamens alternately long and short, the filaments very broad, rounded at apex and with a minute projecting point bearing the anther; longer filaments 3 to 4 mm. long, the shorter 1 to 2 mm. long; anthers 1.5 to 2 mm. long; body of ovary a little longer than the stipe at anthesis and twice as long in fruit.

California Coast Ranges from Lake County to Solano County; also occurring locally in the San Gabriel Mountains of Los Angeles County and on Guadalupe Island off the coast of Baja California.

CALIFORNIA: Lake Co.: 1½ miles west of Oathill Mine, *Wiggins* 6741 (S. T. UC). Napa Co.: head of Moore's Creek, *Tracy* 1450 (UC). Solano Co.: Vaca Mts., 1898, *Platt* (UC); near Signal Station, Vaca Mts., 1938, *Sharpe* (J). Los Angeles Co.: along stream north of Waterman Mt., *Peirson* 2458 (J). BAJA CALIFORNIA: Guadalupe Island, 1896, *T. Brandege* (UC).

Although obviously related phylogenetically to *T. ixioides*, *T. lugens* is not known to have any actual genetic connection with that species. If the two were conspecific, *T. lugens* would be expected to resemble most closely typical *T. ixioides*, which occupies an adjacent area in the Coast Ranges, but actually it is much more similar (except in anther size) to *T. ixioides* var. *analina*, a geographically remote plant of higher altitudes in the Sierra Nevada. It therefore seems best, in order to maintain as nearly as possible a uniform concept of species throughout the genus, to regard *T. lugens* as a distinct species. It is known to occur in Sonoma County but apparently has not been collected there.

The two southern localities of *T. lugens* are so far removed from the principal area of distribution of the species as to be almost incredible, but there is no basis for questioning the authenticity of either record. There is no apparent difference (in dried specimens, it should be noted) between these southern collections and plants of the North Coast Ranges. If *T. lugens* be regarded as the most primitive member of the section *Calliprora*, then this peculiar distribu-

tion can be readily explained by the supposition that the species, once widely distributed, has persisted in a few widely separated localities, and in the intervening territory either has disappeared or has been modified into the more advanced forms represented by *T. ixioides* and its varieties. Some support is given to this theory by the presence in *T. grandiflora* var. *Howellii* of broad apically rounded filaments like those of *T. lugens*. It is therefore possible that such filaments, occurring as they do in two different sections of the genus, are older phylogenetically than the bifurcate filaments of *T. ixioides*.

8. *Triteleia ixioides* (Ait. f.) Greene, Bull. Cal. Acad. 2:142. 1886.

Ornithogalum ixioides Ait. f., Hort. Kew. ed. 2, 2:257. 1811. *Themis ixioides* Salisb., Gen. Pl. 85. 1866. *Milla ixioides* Baker, Journ. Linn. Soc. 11: 383. 1871. *Brodiaea ixioides* Wats., Proc. Am. Acad. 14: 238. 1879, not Hook. (1823). *Hoohera ixioides* Ktze., Rev. Gen. Pl. 1:712. 1891. *Calliprora ixioides* Greene, Man. Reg. S. F. Bay 319. 1894. *Calliprora lutea* Lindl., Bot. Reg. 19: pl. 1590. 1833.

Leaves 3 to 14 mm. wide; scape 1 to 6 dm. tall, smooth or sometimes slightly scabrous near the base; pedicels 1.5 to 7 cm. long, spreading and curved upward; perianth golden yellow, often purplish in drying, the tube 6 to 8 mm. long, acute at base, the segments 10 to 16 mm. long, spreading but not rotate, lanceolate, acute or the inner somewhat obtuse; filaments broad and flat, divergently forked at apex, the longer 4 to 5 mm. long (including the forks), the shorter 2.5 to 3 mm. long; anthers 1.5 to slightly more than 2 mm. long, yellow or occasionally blue, borne on a minute stalk between the forks of the filaments; stipe of ovary shorter than the body.

Near the coast of California from San Mateo County to San Luis Obispo County.

CALIFORNIA: San Mateo Co.: near San Carlos, 1894, Dudley (P); Woodside to Crystal Springs Lake, 1894, Dudley (S); Kings Mountain, 1907, Abrams (S); Portola Valley, Randall 233 (S). Santa Clara Co.: Palo Alto Stock Farm, 1895, Dudley (S); San Juan Hills, San Jose, 1895, Patterson (S); Bald Peak, Mt. Hamilton Range, Dudley 419 (S). Santa Cruz Co.: Buzzard Lagoon, Akey 42 (VTM); Miller's Ranch, on summit between Gilroy and Watsonville, Elmer 4463 (CA, OS, P, S, UC, UO, WS). San Benito Co.: 1¼ miles southwest of Gabilan School, Belshaw 2164 (VTM). Monterey Co.: Pacific Grove, Heller 6841 (P, S, UC, UO); Point Lobos, Eastwood and Howell 6034 (CA); Guadalupe Ranch, Brewer 588 (UC); Miller Canyon, Hall 10071 (P, UC); Tassajara Hot Springs, Elmer 3223 (S). San Luis Obispo Co.: San Carpo Canyon, 1912, Condit (UC).

As here defined, the species *T. ixioides* consists of three groups of plants which, although readily recognizable as a rule, can not be separated by constant characters. Typical *T. ixioides*, a rather infrequent plant, is strictly coastal and widely separated geographically from the two varieties of the interior. It flowers in its native habitat from May to August, and under cultivation at least a month later than var. *scabra*. It is usually found in sandy soil in the shade of oaks or pines. The peculiar brownish purple color which the flowers often assume in drying is seldom if ever seen in the following varieties.

8a. *Triteleia ixioides* (Ait. f.) Greene var. *scabra* (Greene) comb. nov.

Calliprora scabra Greene, Erythea 3: 126. 1895. *Brodiaea scabra* Baker, Gard. Chron.

ser. 3, 20: 459. 1896. *B. ixioides* var. *scabra* Smiley, Univ. Calif. Publ. Bot. 9: 135. 1921, as to name. *Calliprora aurantea* Kell., Proc. Cal. Acad. 2: 20. 1859.

Scape retrorsely hairy near base or sometimes merely scabrous; perianth cream-color or straw-color to deep golden yellow, the tube 4 to 6 mm. long, the segments 10 to 17 mm. long, at anthesis rotate or even slightly reflexed, the inner usually broadly rounded at apex; filaments more or less narrowed upward from the base to below the terminal fork, tending to be contiguous and thus forming a closed tube, the longer 5 to 7 mm. long, the shorter 4 to 5 mm. long; anthers 1 to 2 mm. long; stalk of anther usually black.

Interior of California, on the west side of the Sacramento Valley in Tehama County, and in or near the Sierra Nevada foothills from Butte County to Kern County.

CALIFORNIA: Tehama Co.: Ely, *Jepson* 16335 (J); Dibble Creek near Red Bluff, *Hoover* 4099 (CA, UC). Butte Co.: ridge above Enterprise, *Heller* 11895 (CA, OS, S); 5 miles east of Oroville, *Rose* 33183 (P, UW). Sutter Co.: Marysville Buttes, *Heller* 11365 (CA, OS, S, UC); North Butte, *Ewan* 9575 (J, WS); West Butte, *Ferris* 6326 (P, S); East Butte, *Heller and Brown* 5563 (P, S). Nevada Co.: Penn Valley, *Heller* 13188 (CA, S). Placer Co.: near Newcastle, *Bolander* 4628 (UC); near Loomis, *Applegate* 5366 (S, UC). Eldorado Co.: Coloma, 1928, *Vortriede* (CA); Mosquito, *Belshaw* 2338 (VTM). Sacramento Co.: Fair Oaks, *Ramaley* 11254 (UC); Mormon Island, *Nordstrom* 21 (VTM). Tuolumne Co.: near Indian Creek, *Ferris* 1648 (CA, S); Moccasin Creek, 1895, *Blasdale* (UC). Mariposa Co.: Wawona, *Augustine* 135 (VTM); Mariposa, *Applegate* 6109 (S). Madera Co.: Raymond, *Eastwood* 12557 (CA); near Fresno River between Coarsegold and Raymond, *Eastwood and Howell* 5449 (CA). Fresno Co.: Pine Ridge, *Hall and Chandler* 173 (UC); Piedra, *Hoover* 3980 (CA, S, UC). Tulare Co.: 5 miles southeast of Lindsay, *Munz* 9129 (P, UC); Pine Flat, *Moxley* 561 (UC). Kern Co.: hills west of Woody, *Hoover* 3177 (UC); near Caliente, *Heller* 7623 (S, UC); Fort Tejon, *Parish* 1892 (S).

In the southern Sierra Nevada foothills var. *scabra* is very abundant. North of Mariposa County it is comparatively infrequent. It is most readily recognized by the combination of hairy scape, short perianth tube, rotate or reflexed perianth-segments, and long filaments, but apparently none of these characters can be used to separate all plants of the Sierra Nevada foothills from all those of the coastal region. The anthers tend to be shorter in var. *scabra*, and this feature has been used as a key character by Abrams (1923), but plants from the Sierra Nevada foothills of Tulare County have anthers longer than those of plants from the Santa Cruz Mountains along the coast. The variety *scabra* flowers from March to May, or sometimes later at high altitudes.

There is considerable variation within this variety. In the northern part of its range the flowers are usually of a golden yellow color similar to that seen in typical *T. ixioides*, and the scapes are almost invariably hairy. South of Mariposa County the flowers are commonly pale yellow or straw-color, and toward the southern extremity of the range of the variety the scapes are often merely scabrous. Whenever one of the distinctive features of this variety does not appear, the plants can be identified by the remaining features. Notwithstanding its variability and its resemblance to typical *T. ixioides*, var. *scabra* thus appears to represent a natural unit, and in range corresponds with a number of endemic species of the same region. Among these species may be

mentioned *Brodiaea minor*, *Orthocarpus linearilobus*, *Lessingia nana*, *L. virgata*, and *Lagophylla glandulosa*, all of which are widely distributed in the Sierra Nevada foothills but occur west of the Sacramento River only in the extreme north.

Calliprora aurantea Kell., from the description and from the fact that it was based on a specimen collected at Mariposa, is almost certainly synonymous, as Heller (Muhl. 5:91) has also concluded.³ It has, however, been referred to *T. montana* (*Brodiaea gracilis* Wats.) by Mrs. M. K. Curran (Bull. Cal. Acad. 1:148). It may be noted that Kellogg's specific name is by far the oldest designation and would need to be used if this variety were given specific rank. Because the name is not always appropriate and has been subject to doubt, it seems advisable, in reducing the plant to varietal rank, to adopt a later name which is generally agreed to belong to the form in question.

8b. *Triteleia ixioides* (Ait. f.) Greene var. *analina* (Greene) comb. nov.

Calliprora scabra Greene var. *analina* Greene, *Erythea* 3: 126. 1895. *Brodiaea scabra* (Greene) Baker var. *analina* Baker, Gard. Chron. ser. 3, 20: 459. 1896. *Calliprora analina* Heller, Muhl. 2: 14. 1905. *Brodiaea ixioides* var. *scabra* Smiley, Univ. Calif. Publ. Bot. 9: 135. 1921, as to cited specimens.

Scape never more than 3 dm. tall, smooth or scabrous; perianth light dull yellow, often tinged with smoky blue in drying, the tube 4 to 7 mm. long, the segments 7 to 12 mm. long, spreading but not rotate, each usually with a conspicuous dark mid-vein; filaments usually rather narrow, the longer 3.5 to 5 mm. long, the shorter 2.5 to 3.5 mm. long; shorter filaments sometimes nearly obsolete and then not forked; anthers slightly more than 1 mm. long, usually blue but often white.

Mountains of Jackson County, Oregon, and Siskiyou County, California, southward on both east and west slopes of the Sierra Nevada to Tulare County, California; extending into western Nevada according to Tidestrom (Contr. U. S. Nat. Herb. 25:123).

OREGON: Jackson Co.: north slope of Siskiyou Mts. near line of Southern Pacific Railroad, *Applegate* 699 (S). CALIFORNIA: Siskiyou Co.: Metcalf's Ranch (northeast base of Mt. Eddy), *Heller* 12413 (CA, S); Shasta Springs, *Heller* 7986 (S). Shasta Co.: Goose Valley, *Eastwood* 726 (CA); Montgomery Creek, *Applegate* 5853 (S); Moon Creek, *Johannsen* 180 (VTM, in flower size and stem length approaching var. *scabra*). Tehama Co.: Mineral, 1928, *Grinnell* (J). Plumas Co.: Spanish Peak, *Leiberg* 5157 (UO); Long Lake, *Hall* 9350 (UC). Butte Co.: Jonesville, 1929, *Copeland* (CA, P, S, UC, UO), *H. F. Copeland* 1512 (P, S, UC), *Heller* 12042 (CA); near Stirling, *Heller* 10815 (S, UC); Stirling, *Heller* 13167a (CA, S). Sierra Co.: above Snake Lake, *Barker* 106 (S); Webber Lake, *Doten* 111 (S). Nevada Co.: near Donner Lake, 1884, *Sonne* (UC); near Grass Valley, *Heller* 13216 (CA, S, intermediate toward var. *scabra*). Placer Co.: Blue Canyon, *Walker* 1274 (UC); near Iowa Hill, *French* 62 (VTM). Eldorado Co.: near Echo Camp, *Heller* 12164 (CA, S); Sly Park, *Hall* 11370 (CA). Amador Co.: Ham's Station, *Hansen* 1075 (S); Antelope, *Hansen* 585 (S). Alpine Co.: Carson Pass, *Yates* 3946 (VTM). Calaveras Co.: Mokelumne Hill, *Blaisdell* (CA); Camp Baxter, 1930, *Jussel* (CA). Tuolumne Co.: Cow Creek, *Quick* 1805 (CA); Grohl, *Roseberry* 244 (UC, VTM); Soda Springs, *Brewer* 1775 (UC). Mariposa Co.: 3 miles northwest of Coulterville,

³ The name "*caurantea*," which Heller adopts, was obviously a typographical error.

Hoover 2171 (UC); Yosemite Valley, Abrams 4391 (P, S, UC); Pohono Trail, Schreiber 1730 (S, UC, WS). Mono Co.: Timberline Station, Slate Creek Basin, Clausen 1111 (S, UC); Mammoth Lakes Basin, J. T. Howell 14404 (CA). Madera Co.: Moraine Meadows, Akey 314 (VTM). Fresno Co.: Dinkey Creek, Hall and Chandler 420 (S); Bear Lake, Russell 39 (S). Inyo Co.: Andrews Camp, K. Brandegee (UC). Tulare Co.: Kaweah Meadows, Purpus 5139 (UC); Hockett Meadows, Hall and Babcock 5601 (UC). Dudley 1878 (S), Culbertson (C. F. Baker 4429) (CA, P).

This variety is readily distinguished from both other forms of *T. ixioides* by the small flowers, from typical *T. ixioides* also by flower color, and from var. *scabra* by the slightly ascending perianth-segments and the lack of retrorse pubescence on the scapes. It might be considered a reduced high-altitude form of var. *scabra*, but although it reaches an altitude of 10,000 feet, it is sometimes found in the chaparral belt as low as 2,000 feet, while var. *scabra* in its typical form extends as high as 6,500 feet. Although the two varieties overlap in geographical range to a great degree, apparent intergrades between them are remarkably rare and occur mainly near the northern and southern limits of distribution of the varieties. Unlike var. *scabra*, var. *analina* is most abundant from Mariposa and Tuolumne Counties northward. When cultivated with var. *scabra*, var. *analina* flowers at about the same time, but because it occurs at high altitudes is mostly summer-flowering under natural conditions.

In withering, the forks of the filaments sometimes tend to fold over, and the filaments then appear to be rounded at the apex. Apparently for that reason, this variety has been confused frequently with *T. lugens*, a species which is very similar in general aspect. However, no plants from the Sierra Nevada have been seen in which at least the longer filaments are not forked.

This is undoubtedly the plant mentioned by Tidestrom under the name *Hookera ixioides* as occurring in western Nevada.

9. *Triteleia versicolor* sp. nov.

Scapo 3 ad 6 dm. alto, minute scabro prope basem; pedicellis patentibus, 2 ad 4 cm. longis; perianthio campanulato, in apertione pallide luteo, in anthesi albo, post anthesi saepe purpurascens, tubo 6 ad 7 mm. longis, segmentis 8 ad 10 mm. longis; filamentis longioribus 5 ad 6 mm. longis, brevioribus 3.5 ad 4 mm. longis; furcis filamentarum subparallelibus; antheris albis, 2.5 ad 3.5 mm. longis; stipite ovarii corpore semilongo.

Leaves 7 to 11 mm. wide; scape 3 to 6 dm. tall, densely and minutely scabrous near the base; pedicels spreading, 2 to 4 cm. long; perianth open-campanulate, pale yellow when first opening, white at anthesis, often turning purple after anthesis, the tube 6 to 7 mm. long, the segments spreading but not abruptly so, 8 to 10 mm. long, the outer ovate-lanceolate, acute, the inner obovate, obtuse; filaments flat, thin-margined, the longer 5 to 6 mm. long, the shorter 3.5 to 4 mm. long; forks of filaments nearly parallel; anthers white, 2.5 to 3.5 mm. long; stipe of ovary about half as long as the body.

Coastal region of northern Monterey County, California.

CALIFORNIA: Monterey Co.: Whaler's Knoll, Point Lobos State Park, Mason and Lee 9351 (UC, type).

The fresh flowers of this species are not at all like those of *T. ixioides* in general appearance, differing most notably in shape and color and in the length of the stamens relative to the perianth. The change in color after the flowers open, to which the specific name refers, is very remarkable. It is not surprising to find an additional species in a region already known to be characterized by a large number of endemics. I am grateful to Dr. H. L. Mason for calling my attention to this species and for giving me the opportunity to study living plants under cultivation.

Section 3. TRITELEIA section **Hesperoscordum** (Lindl.) comb. nov.

Hesperoscordum Lindl., Bot. Reg. 15: under pl. 1293. 1830.

10. *Triteleia hyacinthina* (Lindl.) Greene, Bull. Cal. Acad. 2:142. 1886

Hesperoscordum hyacinthinum Lindl., Bot. Reg. 15: under pl. 1293. 1830. *Milla hyacinthina* Baker, Journ. Linn. Soc. 11: 385. 1871. *Hookera hyacinthina* Ktze., Rev. Gen. Pl. 1:712. 1891. *Brodiaea hyacinthina* Baker, Gard. Chron. ser. 3, 20: 459. 1896. *Hesperoscordum lacteum* Lindl., Bot. Reg. 19: pl. 1639. 1833. *Allium lacteum* Benth., Pl. Hartw. 339. 1857. *Milla hyacinthina* var. *lactea* (by error *lacteum*) Baker, Journ. Linn. Soc. 11: 385. 1871. *Brodiaea lactea* Wats., Proc. Am. Acad. 14:238. 1879. *B. hyacinthina* var. *lactea* Baker (by error Wats.), Gard. Chron. ser. 3, 20: 459. 1896. *Hookera hyacinthina* var. *lactea* Jepson, Fl. W. Mid. Cal. 118. 1901. *T. lactea* Dav. & Moxley (by error Wats.), Fl. S. Cal. 87. 1923. *Hesperoscordum Lewisii* Hook., Fl. Bor. Am. 2: 185, pl. 198. 1839. *Veatchia crystallina* Kell., Proc. Cal. Acad. 2: 11. 1859. *Allium Tilingi* Regel, Acta Horti Petrop. 3: 124. 1875. *Brodiaea lactea* var. *lilacina* Wats., Proc. Am. Acad. 14: 239. 1879. *B. hyacinthina* var. *lilacina* Jepson, Fl. Cal. 1:286. 1922. *Brodiaea dissimulata* Peck, Torreyia 32: 147. 1932.

Corm with thick coarsely fibrous coats; leaves 4 to 22 mm. wide; scape 1.5 to 7 dm. tall, smooth or scabrous; pedicels 0.5 to 5 cm. long, usually spreading and curved or bent upward; perianth usually white, sometimes blue or lilac, bowl-shaped, the tube 2 to 4 mm. long, spreading from the base at anthesis, acute at base in fruit, the segments 7 to 12 mm. long, spreading; stamens equal, the filaments dilated toward the base, 2 to 4 mm. long, the anthers 1 to nearly 2 mm. long, white or rarely blue; stipe of ovary very short at anthesis, about half as long as the body in fruit.

Southern British Columbia eastward to northwestern Idaho and southward to San Bernardino County, California; Nevada according to Tidestrom (Contr. U. S. Nat. Herb. 25:123).

BRITISH COLUMBIA: Vancouver Island: Observatory, 1920, Anderson (WS); Esquimalt, Anderson 14a (WS); Oak Park, Victoria, Eastwood 9713 (CA). Mainland: Chilliwack Valley, 1906, Spreadborough (P). WASHINGTON: San Juan Co.: Flat Top Island, Lawrence 106 (WS); Friday Harbor, Zeller 927 (CA). Skagit Co.: Fidalgo City, Flett 2107 (WS); Pass Island, H. W. Smith 957 (UW). Island Co.: Whidby Island, 1897, Gardner (UW, WS). Chelan Co.: Stehekin River, 1923, St. John and Ridout (WS); Peshastin, Sandberg and Leiberger 562 (CA, UC, UW, WS). King Co.: Alki Point, Piper 581 (UW). Jefferson Co.: Marmot Lake, Dickinson 72 (UW). Grays Harbor Co.: Quinalt, Conard 238 (WS); Humptulips City, Lamb 1282 (WS). Thurston Co.: Granger's Prairie, 1905, Townsend (WS); Hawks Prairie, Otis 1924 (T, UW). Kittitas Co.: Mt. Stuart, Elmer 1208 (WS). Yakima Co.: Tieton Basin, Cotton 450 (WS). Klickitat Co.: Bickleton, M. E. Jones 25169 (P, WS). Whitman Co.: Garfield, Wiedman 157 (WS); Pullman, 1893, Piper (S. UW, WS).

IDAHO: Benewah Co.: Forks of St. Mary's River, *Leiberg 1181* (UO). Latah Co.: Pine Creek valley near Farmington, *Sandberg, MacDougal, and Heller 510* (S); Moscow, *Abrams 727* (UC). OREGON: Umatilla Co.: Blue Mountains south of Pilot Rock, *Lawrence 817* (S). Hood River Co.: Hood River, *Henderson 771* (UO). Multnomah Co.: Sauvies Island, 1875, *J. Howell* (UO). Clackamas Co.: Oregon City, *Thompson 851* (S, T); Willamette Falls, *Sheldon 12237* (UO). Marion Co.: Salem, *Thompson 2670* (S, T). Linn Co.: Crabtree, 1915, *Hatch* (OS); near Brownsville, *Henderson 12595* (UO). Benton Co.: 1 mile north of Corvallis, 1912, *Walls and Owens* (OS, S). Lane Co.: Spencer's Butte, *Henderson 16427* (UO). Douglas Co.: Winchester, *Cusick 4085a* (WS); Cow Creek above Riddle, *Henderson 12780* (UO). Curry Co.: Agness, *Henderson 10132* (UO); Harbor, *Peck 8820* (W). Josephine Co.: Eight Dollar Mountain, *Henderson 7203* (UO); Williams Creek, *Applegate 5051* (S). Jackson Co.: Grizzly Peak, *Peck 1358* (W); Pinehurst, *Applegate 4386* (S). Klamath Co.: near head of Denny (Rock) Creek, *Applegate 5160* (S, UC); near Aspen Lake, *Applegate 3397* (S). Deschutes Co.: Sisters, *Peck 4991* (W); Big Meadows, Deschutes River, *Leiberg 510* (P, UC, UO). Crook Co.: "western Crook County," *Cusick 2673* (P, UC, UO). Grant Co.: Austin Ranch, Middle Fork of John Day River, *Henderson 5626* (CA, S, UO). Baker Co.: near head of Burnt River, *Cusick* (UO). Harney Co.: Crane Creek, *R. M. Austin 2230* (S, UC); 5 miles south of Alvord Ranch, *Peck 14007* (W). Lake Co.: between Bull Prairie and Abert Rim, *Andrews 498* (UO); Hart Mountain, *Applegate 7730* (S).

CALIFORNIA: Modoc Co.: Twelve Mile Creek at state line, *Applegate 7660* (S); Fort Bidwell, *Manning 167* (UC). Siskiyou Co.: near Hawkinsville, *Butler 785* (S, UC); Shasta Retreat, 1911, *Condit* (UC). Del Norte Co.: French Hill, *Kildale 9688* (S); Klamath Glen, *Kildale 9519* (S). Humboldt Co.: Eureka, *Tracy 1160* (UC); Englewood, *Constance 930* (J, WS). Trinity Co.: Preacher Meadow, *Eastwood and Howell 4942* (CA); South Fork Mountain, *Kildale 3710* (S). Shasta Co.: Montgomery Creek, *Eastwood 844* (CA); near Middle Creek Station, *Heller 7911* (S, UC). Lassen Co.: Honey Lake Valley, *Davy 3386* (UC). Tehama Co.: near Morgan, *Hall and Babcock 4343* (UC); 7 miles south of Corning, *Heller 12997* (CA, S). Plumas Co.: Prattville, *Heller and Kennedy 8791* (CA, S); Taylor Creek, *Wagner 305* (S). Butte Co.: 3 miles north of Chico, *Hoover 3245* (CA, UC); 8 miles north of Oroville, *Heller 11302* (CA, OS, S, UC). Mendocino Co.: Anderson Valley, *Bolander 4826* (UC); Fort Bragg, *Duncan 252* (S). Lake Co.: Sulphur Banks, *Eastwood and Howell 5644* (CA); Binkley Ranch, *Jussel 316* (CA, UC). Yuba Co.: Los Vergils, *Eastwood 10537* (CA). Sierra Co.: Salmon Lake, 1918, *Sutcliffe* (CA); Loyalton, *Eastwood 7894* (CA). Nevada Co.: Donner Lake, *Sonne 310* (S); Nevada City, *Eastwood 600* (CA). Placer Co.: Emigrant Gap, *M. E. Jones 3513* (CA, P); Lincoln, *Ramaley 11105½* (UC). Eldorado Co.: Fallen Leaf Lake, *Eastwood 1102* (CA); 1½ miles north of Lover's Leap, *Belshaw 2633* (S, UC). Amador Co.: Caminetti Ranch, near Jackson, *Mulliken 110* (P, S, UC). Sacramento Co.: Carmichael, *Ramaley 11227* (UC); near North Sacramento, *Applegate 5372* (S). Solano Co.: Vacaville, *C. F. Baker 2926* (P, UC); Suisun, *Eastwood 10406* (CA). Napa Co.: Napa Wye, *Jepson 18784* (J). Sonoma Co.: Kenwood, 1893, *Michener and Bioletti* (UC). Marin Co.: near Olema, *Henderson 15439* (UO); Corte Madera, 1886, *Rattan* (S). San Joaquin Co.: near Peters, *Stanford 950* (P, S). Calaveras Co.: Lancha Plana, *Roseberry 139* (UC, VTM); Calaveras Big Trees, 1880, *Cleveland* (SD). Tuolumne Co.: Brightman Flat, *Hoover 4159* (CA, S, UC); Spring Gulch, *Williamson 151* (CA, P, S). Stanislaus Co.: Warnerville, *Hoover 1049* (UC). Alameda Co.: Peralta Park, *Davy 2966* (UC). San Mateo Co.: road from Woodside to Crystal Springs, 1906, *McMurphy* (S). Santa Clara Co.: Stanford University, *Abrams 2374* (S); Hall's Valley, *Pendleton 840* (UC). Santa Cruz Co.: Graham Hill, 1937, *C. A. Reed* (CA). Monterey Co.: Pacific Grove, 1907, *Patterson and Wiltz* (S, UC); San Antonio River (upper edge of Milpitas Ranch), *Hall 9980* (UC). Mariposa Co.: Yosemite Valley, *Abrams 4671* (S). Merced Co.: Hayward, *Carlson 400* (UC, VTM); 7 miles north of Merced, *Hoover 534* (UC). Fresno Co.: Corlew Meadow, *Bullard 113* (VTM); Pine Ridge, *Hall and Chandler 582* (UC). Tulare Co.: 4 miles north of Visalia, *Hoover 922* (UC); near Milo, 1900, *Dudley* (S). San Bernardino Co.: Camp Baldy, 1919, *Potter* (LA).

As would be expected with a species of such wide distribution, *T. hyacinthina* shows considerable variability. The original description, citing plants collected by Douglas in the "north-west of America," evidently applies to the commonest form of the species. The form represented by *Hesperoscordum lacteum* Lindl., which was based on plants raised from bulbs obtained in California by Douglas, appears to differ only in having longer pedicels. The latter is nearly restricted to California and often grows in relatively dry situations. An extreme form with unusually rigid scabrous scapes and without vegetative multiplication is common in rather dry places in the Great Valley. In wet places in the same region is occasionally found the typical form of the species, which is identical in flower structure. The various forms thus do not seem to represent well marked geographical varieties.

Throughout the range of this species, the great majority of plants have white flowers. There are, however, a few interesting color variations of restricted distribution. Plants with lilac flowers, representing *Brodiaea lactea* var. *lilacina* Wats., are found in northwestern California and southwestern Oregon. Blue flowers are occasional in the northern Sierra Nevada, and one collection from Santa Cruz County, California, has purple flowers. Usually, if not always, colored flowers occur mixed in the same colonies with white flowers and are therefore not taxonomically significant. *Brodiaea dissimulata* Peck is described as having pale yellow flowers, but in the type specimens, which I have seen, the flowers appear to be white and are not discolored to an unusual degree.

10a. *Triteleia hyacinthina* (Lindl.) Greene var. *Greenei* nom. nov.

T. lilacina Greene, Bull. Cal. Acad. 2: 143. 1886. *Brodiaea lilacina* Baker, Gard. Chron. ser. 3, 20: 459. 1896. *Hesperoscordum lilacinum* Heller ex Abrams, Ill. Fl. Pac. St. 1: 401. 1923. Not *Brodiaea lactea* var. *lilacina* Wats., or *B. hyacinthina* var. *lilacina* Jepson.

Interior of perianth-tube covered with hyaline vesicles (these not evident after drying); filaments filiform, not dilated; anthers blue.

Northern Sierra Nevada foothills and their bordering plains from Tehama County to Tuolumne County, California.

CALIFORNIA: Tehama Co.: northeast of Red Bluff (no collection made). Butte Co.: plains north of Chico, R. M. Austin 36 (UC); Chico, Ramaley 11208 (UC); Chico—Oroville road 11 miles from Chico, Heller 11285 (CA, OS, S, UC). Placer Co.: Auburn, 1915, Hawver (CA). Calaveras Co.: hills west of San Andreas, Mason 5556 (UC). Tuolumne Co.: Mountain Pass (in serpentine), Ferris 1587 (S); 2 miles west of Chinese Camp, Hoover 1950 (CA, UC).

In vegetative characters and general structure of the flower, this interesting plant is exactly like the dry-land form of *T. hyacinthina* which is common in the same region. The anthers appear to be white in a few of the specimens seen but probably tend to fade in drying. Blue anthers in typical *T. hyacinthina* have been observed in the blue-flowered form of the northern Sierra Nevada. The collection of var. *Greenei* from Placer County has filaments slightly flattened toward the base though hardly dilated and thus seems to vary toward typical *T. hyacinthina*. The conspicuous hyaline vesicles of the perianth are not evident in typical *T. hyacinthina* as it occurs in the Sierra Nevada foothills,

but the description of *Veatchia crystallina* Kell., which appears to be referable to typical *T. hyacinthina*, suggests that such vesicles may not be peculiar to the variety. In view of these facts, it seems best for the present to place this plant in varietal rank. In order to avoid confusion with *Brodiaea lactea* var. *lilacina* Wats., a mere color form of *T. hyacinthina*, this variety is here renamed in recognition of the botanist who first described it. *Triteleia lilacina* Greene was based on a specimen collected in Amador County, California, by Curran and was described as having "lilac-purple" flowers. Although I have seen only plants with white flowers (often tinged with blue in drying), there may be the same variability of color which is seen in typical *T. hyacinthina*, or in describing dried specimens an error in regard to color could easily be made. The variety *Greenei* usually grows in shallow soil among volcanic rocks.

11. *Triteleia Lemmonae* (Wats.) Greene, Bull. Cal. Acad. 2:141. 1886.

Brodiaea Lemmonae Wats., Proc. Am. Acad. 20: 376. 1885.

Leaves 2 to 6 mm. wide; scape 8 to 25 cm. tall, scabrous near the base or sometimes smooth; bracts often purplish; umbels usually compact, the pedicels 7 to 25 mm. long; perianth apparently yellow ("deep orange" according to original description), the tube spreading from the base, 2.5 to 3 mm. long, the segments continuous in the same direction, 7 to 9 mm. long; stamens in one row, equal, the filaments about 3 mm. long, very slightly dilated toward the base, the anthers about 2 mm. long; body of ovary 3 or 4 times as long as the style.

Mountains of southern Coconino County and northern Gila County, Arizona.

ARIZONA: Coconino Co.: Spring Valley near Sitgreaves Mt., *Lemmon 3347* (UC); Mogollon Rim, Oak Creek Canyon Road, *A. and R. A. Nelson 2098* (UC); Mormon Lake, *MacDougal 54* (UC). Gila Co.: Young to Payson, *Pebbles and Smith 13288* (P). County not known: "Laguna Indian Village," 1884, *Lemmon* (UC).

As it is the only representative of the genus in Arizona, this localized plant is widely separated geographically from all other species. The original collection was made on Oak Creek near Flagstaff by Mr. and Mrs. J. G. Lemmon. *Triteleia Lemmonae* is so similar to *T. hyacinthina* that it is difficult to find morphological characters which will distinguish it from all forms of that species. Because of its flower color and range, however, it appears to be distinct. It has been collected in flower from late May to August.

12. *Triteleia montana* nom. nov.

Brodiaea gracilis Wats., Proc. Am. Acad. 14: 238. 1879. *T. gracilis* Greene, Bull. Cal. Acad. 2: 141. 1886; not *T. gracilis* Phil. (1873, acc. to Index Kewensis). *Hookera gracilis* Ktze., Rev. Gen. Pl. 1: 712. 1891.

Leaves 2 to 5 mm. wide, usually solitary; scapes 5 to 20 cm. tall, more or less scabrous; pedicels 0.5 to 3 cm. long, in fruit spreading and curved upward at apex; perianth yellow, often turning purple in age, the tube slender, 4 to 5 mm. long, the segments somewhat spreading, 8 to 10 mm. long; stamens inserted at the same level, equal, the filaments filiform, not at all dilated down-

ward, 5 to 6 mm. long; anthers yellow, 1 to 1.5 mm. long; stipe of ovary about equalling the body.

Sierra Nevada of California from Plumas County to Mariposa County.

CALIFORNIA: Plumas Co.: Drakesbad, *Parks* 0244 (UC); Prattville, *Heller and Kennedy* 8816 (S); Long Valley, *Eastwood* 14626 (CA); Mooreville Ridge, *Axelrod* 43 (VTM). Butte Co.: Jonesville, 1932, *H. F. Copeland* (UC). Nevada Co.: near Twin Valley, 1897, *Sonne* (UC); Hobart Mills, 1925, *Drew* (S). Tuolumne Co.: Conness Creek, *Jepson* 3359 (J), 4482 (J); between Crane Flat and Tuolumne Big Trees, *Abrams* 4700 (S). Mariposa Co.: Lake Tenaya, *Hall and Babcock* 3523 (UC), *Eastwood* 459 (CA); Tamarack Flat, *Jepson* 8350 (J); El Capitan summit, *Jepson* 4361 (J).

The name here given to this species refers to the fact that it is strictly montane, occurring at altitudes between 4,000 and 9,000 feet and flowering in June and July. It is apparently common in Plumas County in the northern Sierra Nevada. The type was collected on Spanish Peak, Plumas County, by Mrs. R. M. Austin. Between Nevada County and Yosemite National Park, where it frequently has been collected in the mountains between the Tuolumne and Merced Rivers, there is a rather extensive area where the species does not occur.

13. *Triteleia Hendersoni* Greene, Pitt. 1:164. (Feb. 4) 1888.

Brodiaea Hendersoni Wats., Proc. Am. Acad. 23: 266. (May 29) 1888.

Leaves 3 to 12 mm. wide; scape 12 to 35 cm. tall, smooth or slightly scabrous near the base; bracts narrow, acuminate, 1 to 3 cm. long; pedicels 1.5 to 4 cm. long, in fruit spreading and curved upward at the apex; perianth yellow, fading and often tinged with blue in drying, the tube slender-funnelform, 6 to 7 mm. long, the segments apparently widely spreading, 13 to 16 mm. long, each with a dark purple mid-vein; stamens equal or very slightly unequal, the filaments narrowly subulate, 3 to 4 mm. long, the anthers 1.5 to 2 mm. long, blue or sometimes white; stipe of ovary at anthesis nearly twice as long as the body.

Southwestern Oregon from southern Lane County to Josephine and Jackson Counties; perhaps in adjacent California.

OREGON: Lane Co.: Cottage Grove, *Peck* 4988 (W); 3 miles south of Cottage Grove, *Peck* 14929 (W). Douglas Co.: near Riddle, *Gale* 194 (S, T); Cow Creek Canyon above West Fork, *Henderson* 12335 (UO); Glendale, *T. Howell* 1274 (OS, UO, WS), 1887, *T. Howell* (UC, type collection). Josephine Co.: Wolf Creek, 1884, *T. Howell* (T, UO); 2 miles west of Merlin, 1928, *Leach* (UO); Provost, *Applegate* 5049 (S); Cedar Flat trail, Williams Creek, *Applegate* 5109 (S); Mt. Grayback, *Thompson* 13004 (T, W, WS); near Waldo, *J. Howell* 57 (UO). Jackson Co.: Buck Rock, 1895, *Applegate* (S); Ashland, *Peck* 1362 (W); Pinehurst, *Applegate* 4346 (S, UC), 4393 (S, UC); Siskiyou summit, *Eastwood and Howell* 2768 (CA). CALIFORNIA (?): "Northwest California," 1879, *Rattan* (S).

Within its restricted range, *T. Hendersoni* is evidently common. The long narrow bracts as well as the structural details of the flower aid in its recognition. The species was apparently described independently by Watson and by Greene. Under the original description, Greene mentioned the fact that Howell had distributed specimens under the name *Brodiaea Hendersoni*. This name was

perhaps supplied to Howell by Watson before its publication. Greene based his species on Howell's collection of 1887 from Glendale, Douglas County, but Watson cited collections made by Henderson near Ashland, Jackson County, in 1884 and 1886.

13a. *Triteleia Hendersoni* Greene var. *Leachiae* (Peck) comb. nov.

Brodiaea Leachiae Peck, *Torreyia* 32: 147. 1932.

Perianth white, often suffused with blue.

Along the Rogue River in Curry County, Oregon.

OREGON: Curry Co.: Illahee, *Applegate* 7206 (S); Shasta Costa Ranger Station, *Applegate* 7150 (S, UC); Rogue River above Agness, *Henderson* 10131 (UO).

This plant differs from *T. Hendersoni* only in flower color. Because the flowers of typical *T. Hendersoni* tend to fade and frequently assume a bluish tint in drying, herbarium specimens of the two are indistinguishable, so that it is necessary to depend upon the statement of the collectors as to the identity of the plants. Although it does not seem advisable ordinarily to name color forms as varieties, there is in this case well marked geographical separation. Typical *T. Hendersoni* has never been found in Curry County.

14. *Triteleia Bridgesii* (Wats.) Greene, *Bull. Cal. Acad.* 2:141. 1886.

Brodiaea Bridgesii Wats., *Proc. Am. Acad.* 14:237. 1879. *Hookera Bridgesii* Ktze., *Rev. Gen.* 1:712. 1891.

Leaves 3 to 10 mm. wide; scape 1 to 5 dm. tall, retrorsely scabrous or even hairy near the base, usually smooth above, or in Coast Range plants smooth throughout; pedicels 1.5 to 9 cm. long, in fruit tending to spread and abruptly bent upward at apex so that the perianth stands erect; perianth lilac or blue, the tube 17 to 25 mm. long, gradually expanding from the extremely slender base, the segments 10 to 20 mm. long, spreading at anthesis; stamens inserted at mouth of perianth-tube, the filaments triangular, attenuate upward, 3 to 4 mm. long, the anthers blue, 3.5 to 4.5 mm. long; stipe of ovary 3 to 4 times as long as the body at anthesis, about twice as long in fruit.

Coast Ranges from Curry County, Oregon, to northern Humboldt County, California, and southeastward in the Sierra Nevada foothills to Mariposa County, California.

OREGON: Curry Co.: Rogue River below Agness, *Applegate* 7140 (S, UC); Gold Beach, *Henderson* 11671 (UO); Pistol River Mountain, *Thompson* 4576 (S, W); Brookings, *Henderson* 7200 (UO). CALIFORNIA: Del Norte Co.: Patrick Creek, *Eastwood* and *Howell* 3636 (CA); Douglas Park, *Thompson* 4494 (S, T), 12912 (T, WS); Regua, *Kildale* 9503 (S). Humboldt Co.: Klamath River at Bluff Creek, *Kildale* 9739 (S); Hupa, *Goddard* 37 (UC); Brannan Mt., *Abrams* 7127 (S). Trinity Co.: Salyer, *Kildale* 9214 (S). Shasta Co.: Long Gulch, *Johannsen* 127 (VTM); Happy Valley, 1910, *W. W. Jones* (UC). Tehama Co.: 11 miles north-east of Red Bluff, *Jepson* 16353 (J). Butte Co.: Near Cohasset, *Heller* 11903 (CA, OS, S); near Clear Creek school house, *Heller* 11379 (CA, OS, S, UC). Yuba Co.: Smartsville, 1923, *Cramie* (CA). Nevada Co.: near Kress, *Hall* 10164 (S, UC); Bear River, *Hall* 10148 (P, UC). Placer Co.: Gold Run, 1891, *Sonne* (UC). Eldorado Co.: White Rock Canyon, *Belshaw* 2337 (VTM); Simpson's Ranch, Sweetwater Creek, 1907, *K. Brandegee* (UC). Amador Co.: Pine Grove, *Hansen* 1253 (S). Calaveras Co.: near Angels Camp, *Davy* 1485 (UC, UO). Tuolumne Co.: Spring Gulch, *Williamson* 67 (CA, P, S). Mariposa Co.: between Mariposa

and Briceburg grade, *Bacigalupi* 1852 (S); west side of Mariposa Valley, 1894, Congdon (S, UC).

The superficial similarity of this species to *T. laxa* is remarkable. Herbarium specimens of the two species often can be distinguished only by examination of the stamens. However, in fresh flowers the perianth-segments of *T. Bridgesii* spread abruptly from the mouth of the tube, unlike those of *T. laxa*. The triangular filaments of *T. Bridgesii* indicate a relationship to *T. hyacinthina*. *Triteleia Bridgesii* shows a development of hyaline vesicles in the perianth-tube similar to that seen in *T. hyacinthina* var. *Greenei*, although not so well marked. An illustration of this species has been published in "Addisonia" (19:11, pl. 614. 1935).

Triteleia Bridgesii is one of the numerous species which occur mainly in areas of serpentine rocks, although it is not strictly limited to such areas. Where observed with *T. laxa* in the Sierra Nevada foothills, it flowers a month later than that species, beginning in the middle of May. The original collection was made by Bridges at an unknown locality, in the Sierra Nevada foothills according to Watson. Plants from Humboldt County have unusually long flowers, a fact which accounts for the wide range in the measurements given for the perianth in the above description.

Excluded Species

Although the available material is very scanty, all South American species formerly referred to *Triteleia* seem to belong properly to *Nothoscordum*. They apparently have been excluded from that genus in the past only because of the shape of the perianth, but the great variability in that feature within such obviously natural genera as *Triteleia* and *Dichelostemma* convinces me that shape of perianth is of very little value as a means of generic distinction in the Alliioideae. Mention should also be made of the genus *Tristagma* Poepp., to which many of these species seem to be referable on the basis of the descriptions of the genus in such works as Benthams and Hooker's "Genera Plantarum" and Engler and Prantl's "Natürlichen Pflanzenfamilien." No material of the type species of *Tristagma* has been available for comparison. It is therefore impossible to reach definite conclusions at this time.

Triteleia aurea Lindl.—*Nothoscordum aureum* (Lindl.) Johnston & Parodi.
Triteleia Berteri Kunth.
Triteleia bivalvis Lindl.
Triteleia brevipes Kunze.
Triteleia caerulea André.
Triteleia conspicua Baker.
Triteleia Gaudichaudiana Kunth.
Triteleia gracilis Phil.
Triteleia graminifolia Presl.
Triteleia Leichtlinii (Parker) Nichols.

Triteleia hirtella Kunth—*Nothoscordum hirtellum* (Kunth) Herter.
Triteleia Palmeri (Wats.) Greene. See following description of new genus.
Triteleia palagonica Baker.
Triteleia Poeppigiana Gay.
Triteleia porrifolia Poepp.
Triteleia Sellowiana Kunth.
Triteleia sessilis Phil.
Triteleia uniflora Lindl.
Triteleia violacea Kunth.

Description of New Genus

Triteleiopsis gen. nov.

Planta non alliacea. Cormus parvus, cum tunica fibrosa straminea, in anthesi in plures parvos cormos in tunica inclusos dividens. Caulis base foliosus, teres,

robustus (7 ad 10 mm. diametro), glaucus, praesertim supra. Folia 3 ad 8, alternantia, congesta, plana, base expansa et membranacea, in axillis parvos cormos ferentia. Umbella multiflora. Bractae involucales parvae, scariosae, acuminatae. Tubus perianthii segmentis aequilongus. Segmenta perianthii cum appendiculis transversis squamiformibus alternantia. Filamenta supra in tubo perianthii inserta, gracilia, teretia, papillata. Antherae basifixae. Stigma non evidenter lobatum. Ovarium ad stipitem sensim attenuatum. Capsula loculicidalis, apice rotundata, perianthium aequans. Semina (immatura) nigra, elongata, compressa, minute asperata.

Plant without alliaceous odor. Corm small, with straw-colored fibrous coat, at flowering time dividing into several cormlets clustered around the base of the stem and enclosed in the coat of the old corm. Stem leafy at base, terete, stout (7 to 10 mm. at point of maximum diameter), pithy, glaucous, especially above. Leaves 3 to 8, alternate, crowded, flat, expanded and membranous at base, bearing cormlets in the axils, apparently carinate above the base. Umbel many-flowered. Involucral bracts, scarious, acuminate. Pedicels jointed. Perianth-tube equalling the segments in length. Perianth-segments alternating with transverse scale-like appendages having no apparent connection with the stamens. Filaments inserted in upper part of perianth-tube, slender, terete, papillate. Adnate portion of filaments evident as internal ridges to base of perianth-tube. Anthers basifixed. Stigma not evidently lobed. Ovary gradually narrowed to a slender stipe. Capsule loculicidal, rounded at apex, equalling the withered perianth. Seeds (immature) black, elongated, thin and flat, the surface minutely and irregularly roughened.

Only one species is known:

***Triteleiosis Palmeri* (Wats.) comb. nov.**

Brodiaea Palmeri Wats., Proc. Am. Acad. 24: 78. 1889. *Triteleia Palmeri* Greene, Pitt. 1:292. 1889.

In form and superficial aspect the flowers are similar to those of *Triteleia*, but this genus differs so much in certain details of flower structure and especially in vegetative characters from all species of *Triteleia* that it must be regarded as distinct. Its inclusion in any other genus known to me would result in an obviously unnatural grouping of species. A table summarizing the differences between *Triteleiosis* and the two genera to which it has been referred is appended. The determination of the generic characters was made possible through the help given by Dr. I. L. Wiggins, who has given me some exceptionally good dried specimens, and by Mr. Frank F. Gander, who sent fresh flowers collected by Mr. C. F. Harbison. The plants grow in loose sandy soil. Apparently each corm retains its identity for only one year, the plants flowering each year from the cormlets formed during the previous season within the old corm-coats and in the axils of the leaves. *Triteleiosis Palmeri* is apparently restricted to the middle portion of Baja California. The following collections have been seen.

BAJA CALIFORNIA: Arroyo del Rosarito, 30 miles south of Punta Prieta, Harbison 11811 (S, SD); coast near Ascension Island, 1897, T. Brandegee (UC); San Jorge, 1889, T. Brandegee (S); 22 miles south of Pozo Alemán, Wiggins 7860 (S); 24 miles north of San Ignacio, Wiggins 7885 (S).

Table Showing the Principal Characters Distinguishing *Triteleopsis* from *Triteleia* and from *Brodiaea*.

	<i>Brodiaea</i>	<i>Triteleia</i>	<i>Triteleopsis</i>
Corm	Coat dark brown. Producing bulblets or offsets at base or not dividing.	Coat straw-color. Dividing by fission, the new corms enclosed in separate coats, or not dividing.	Coat straw-color. Freely dividing, the young corms enclosed together in the old coat.
Scape or stem	Slender (1 to 2 mm.).	Rather slender (about 1 to 5 mm.).	Stout (7 to 10 mm.).
Leaves	Two to five. Arising directly from corm. Neither keeled nor channeled.	One or two. Arising directly from corm. Keeled beneath, doubly channeled above.	Three to eight. Attached to stem, alternate. Apparently keeled above the expanded base, not evidently channeled.
Internal transverse appendages of perianth.	Absent.	Absent.	Present.
Filaments	Smooth.	Smooth.	Papillate.
Anthers	Nearly basifixed. Appressed to style. Sagittate at base.	Versatile. Distant from style. Not evidently sagittate.	Basifixed. Distant from style. Entire at base.
Stigma	With conspicuous recurving lobes.	With small inconspicuous lobes.	Not evidently lobed.
Capsule	Sessile or obscurely stipitate. Of firm texture.	Distinctly stipitate. Of thin texture.	Distinctly stipitate. Of thin texture.
Seeds	Slightly longer than thick. Turgid. Striate-reticulate.	Slightly or not at all longer than thick. Turgid. Granulate or granulate-reticulate.	Much longer than thick. Flattened (immature). Neither striate nor granulate, perhaps smooth when mature.

REFERENCES

- ABRAMS, L. R. 1923—Illustrated Flora of the Pacific States, 1.
 BAKER, J. G. 1871—Revision of the Genera and Species of Herbaceous Capsular Gamophyllous Liliaceae. Journ. Linn. Soc. 11:349-436.
 GREENE, E. L. 1886—Some Genera Which Have Been Confused under the Name *Brodiaea*. Bull. Cal. Acad. 2:125-144.
 HOOVER, R. F. 1939—A Definition of the Genus *Brodiaea*. Bull. Torr. Club 66:161-166.
 JEPSON, W. L. 1922—Flora of California, vol. 1, part 6.
 KUNTH, K. S. 1843—Enumeratio Plantarum, vol. 4.
 MACBRIDE, J. F. 1918—Further New or Otherwise Interesting Liliaceae. Contr. Gray Herb. 56:1-20.
 PIPER, C. V. 1906—Flora of the State of Washington. Contr. U. S. Nat. Herb., vol. 11.
 WATSON, S. 1879—Revision of the North American Liliaceae. Proc. Am. Acad. 14:213-288.

The Developmental History of Cedar Creek Bog, Minnesota*

Raymond L. Lindeman

The Anoka Sand Plain of east central Minnesota is liberally sprinkled with lakes, bogs and marshes, representing innumerable phases of hydrarch succession. One of the most interesting areas of this region is known as the Cedar Creek Bog; it is located astride of the Anoka-Isanti county boundary, Range 23W, Township 34N, Section 27. The character of this bog was first recognized in 1931 by Dr. W. S. Cooper, during an aerial survey of the Anoka Sand Plain. Terrestrial explorations corroborated his surmise that the bog represented an advanced successional stage of what had once been a much larger lake, formed in an ice-block depression of pitted outwash.

Under the inspiration of Dr. Cooper and the cooperation of Dr. Samuel Eddy, several ecological studies have been initiated on the Cedar Creek Bog, the results of which are to be judged from time to time under the collective title "Ecological Studies of a Senescent Lake."

Geology

The late-glacial history of the Anoka Sand Plain has been carefully studied by W. S. Cooper (1935). During the Middle Wisconsin glaciation a lobe from the Patrician ice center pushed southward across the Anoka area, bringing with it rock fragments from the igneous formations around the western end of Lake Superior as well as quartzite and small amounts of limestone from other formations south of the Lake Superior Basin (Leverett & Sardeson, 1932, p. 40). The resultant Patrician drift consists of a rather loose-textured reddish till. The essentially non-calcareous nature of this drift is important to us here because of its later contribution to the outwash sand of the Anoka Sand Plain.

During the Late Wisconsin glaciation ice from the Keewatin center, bearing much calcareous material, moved southeastward across central Minnesota until it encountered the high terminal moraines of the Patrician drift, as shown in Fig. 1. The main body of the ice pushed southward to form the Des Moines Lobe, but a thin sheet known as the Grantsburg Sublobe was deflected north-eastward across the Anoka area.

The advancing ice front of the sublobe pushed before it the precursor of the present Mississippi river; the waters of this river became impounded to form glacial Lake Grantsburg, which found an outlet through the channel of the

* This is the first paper of a series, "Ecological Studies of a Senescent Lake," describing various ecological aspects of the Cedar Creek Bog. The second paper, entitled "Surface Level Fluctuations in Cedar Creek Bog" by Murray F. Buell and Helen Foot Buell, appears in *Ecology*, Vol. 22, 1941.

modern St. Croix river. Upon stagnation and recession of the Grantsburg Sublobe, the river gradually migrated back across the plain of exposed till and stagnant ice, but continued for a considerable time to empty into the St. Croix channel at a point near Taylor's Falls. When finally the ice had receded sufficiently to expose the original channel, the Mississippi River reverted to approximately its previous course. This southwestward migration of the river, according to Cooper, left the interior of the Sublobe as a hodge-podge of small areas of level till, fragments of moraine, and great expanses of outwash sand; Cooper named this outwash area the Anoka Sand Plain.

The material comprising the outwash deposit, according to the Anoka County soil survey (Smith, Nesom and Roth, 1916), consists of fine sand. Cooper (1935) subjected samples to mechanical analysis and found that these

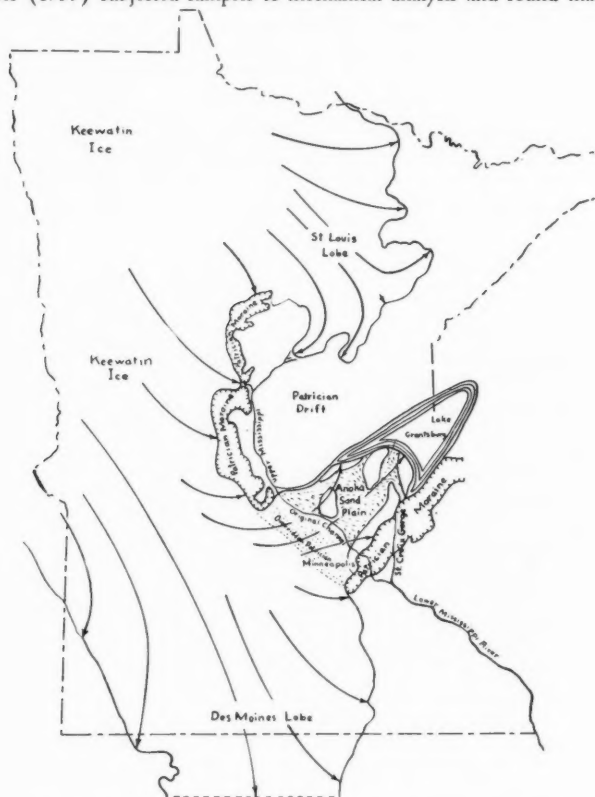


Fig. 1. Formation of the Anoka Sand Plain (after Cooper, 1935).

averaged 78% fine and very fine sand. Samples from the Cedar Creek Bog region contained 40-60% of very fine sand ($>0.1\text{mm}$); no pebbles or coarse rock fragments have been found in this area.

The Cedar Creek Bog region (see Fig. 2) presents an interesting example of pitted outwash. According to Thwaites (1937):

Pitted outwash is formed only within the area occupied a comparatively few years before by ice. Isolated blocks of ice persisted longest in pre-existing depressions such as the kettles of buried terminal deposits and preglacial or interglacial valleys. In many places outwash must have been deposited on top of a more or less continuous sheet of stagnant ice of variable thickness. Deposition of sand and gravel went on so rapidly that it buried the ice masses or sheets in whole or in part, thus retarding their melting.

Such an explanation might very well account for the intricate pattern of upland and peat areas shown on the map (Fig. 2); it should be remembered that the ice blocks must have been quite variable in size and that some of the "channels" observed are quite superficial, perhaps in some cases the result of subsequent stream work.

The topography immediately surrounding the Cedar Creek Bog (shown in Fig. 3, which is an enlargement of the quadrangle marked in Fig. 2) indicates that the central part of the basin east of Second Island and Crone Island is almost certainly due to the melting of a single large block of ice. When this block melted it formed a "drainage" lake more than 12 meters in depth, representing the earliest stage of what is now called Cedar Bog Lake.

Vegetational Succession

Since the glacial period the basins of kettle-holes and depressions have mostly been filled with peat, although some still contain ponds or lakes. The surface peat has been formed largely by sedges, especially along the drainage channels; many of the poorly drained pits, on the other hand, have developed into tamarack or spruce bogs with thick layers of *Sphagnum* and forest peat beneath the trees. The Cedar Creek Bog is unique in this region in having developed an extensive bog forest of white cedar or arbor vitae (*Thuja occidentalis*), which has been encroaching upon the original basin of Cedar Bog Lake.

The various stages of hydrarch succession in the Cedar Bog are represented by successively peripheral girdles of vegetation encircling the open water. In the lake itself great masses of such pondweeds as *Najas flexilis*, *Ceratophyllum demersum* and *Potamogeton zosteriformis*, together with an abundance of epiphytic *Gloeotrichia*, develop during each growing season. Serotinal blooms of blue-green algae occur during certain years. The incomplete decomposition of this luxuriant flora contributes greatly to the formation of sedimentary ooze and the filling in of the open water area.

At the inner margin of the sedge mat grow amphibious species which are especially adapted to a substratum offering very little support. Most of the lake is bordered by an invading front of *Decodon verticillatus* (swamp loosestrife), a plant rare in Minnesota but very abundant in the Cedar Bog. *Decodon* is partly supported in the tenuous ooze by cork-like aerenchyma on the roots and



Fig. 2. Photo-map of Cedar Bog Lake Region (Sept. 21, 1938), showing relation of upland and peat areas in pitted outwash. The meandering Cedar Creek is shown on the left. Photograph by courtesy of the federal Soil Conservation Administration.

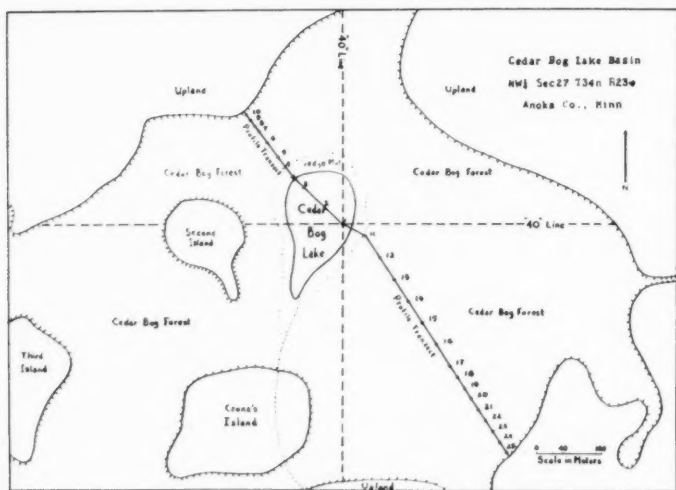


Fig. 3. Enlarged map of the quadrangle outlined in Fig. 2.

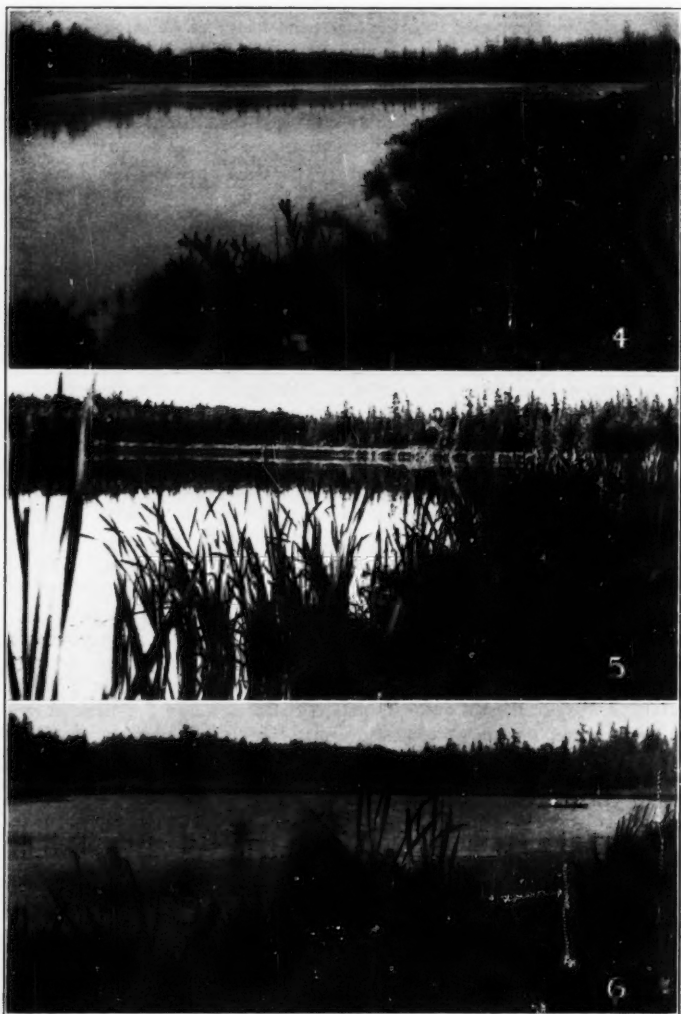
stems. *Typha latifolia* (cattail) is not so well adapted for marginal invasion and is typically interspersed with the peripheral fringe of *Decodon*; its success on the mat seems to vary inversely with high water level. There thus appears to be a constant cyclic struggle for marginal dominance between *Typha* and *Decodon*. During years of abundant rainfall *Decodon* controls the invasion; during drier climatic periods, due to lowering of the lake level, *Decodon* gives way to *Typha*. Such cyclic changes have taken place during the past ten years.

When the lake was first observed in 1931, *Decodon* everywhere dominated the margin, as indicated in the photograph (Fig. 4) taken by W. S. Cooper during the summer of that year. Murray F. Buell, who visited the lake at intervals from 1932 to 1935, reported that the water level was high and *Decodon* abundant in 1932, but that during the summers of 1933 and 1934 the lake level dropped so much that a great "soupy mud flat" extended out from the margin for 15 to 25 meters. Water was much higher in 1935, but had dropped again in 1936 when the present author first saw the lake. These summer drouths spelled hard times for the *Decodon*, so that by the summer of 1937 (Fig. 5) *Typha* seemed to dominate the entire margin. Recent years have been much more normal, and at present (1940) *Decodon* seems to be regaining control of the lake margin, as suggested by Fig. 6.

The rapidity of marginal invasion is attested by two measurements: in May, 1935, Buell measured the distance from a marker on the sedge mat (designated "X" in Fig. 3) to the edge of open water as 2.8 meters; in May, 1940, the author found the water's edge to be 3.75 meters from this marker. Marginal invasion, due largely to the proliferation of *Decodon*, had encroached on the lake a radial distance of practically 1 meter in 5 years. At this tremendous rate the lake will have become a bog swale within 250 years.

The marginal mat vegetation supports many other plants besides *Decodon* and *Typha*, including sedges, grasses, other herbs, ferns and mosses. Scattered willows and alders also occur, and young tamaracks are abundant along the peripheral margin. Heaths and sphagna, so characteristic of bog mats in other regions, are not prominent near the Cedar Bog margin; bog birch (*Betula pumila* var. *glandulifera*) occurs locally. "Soil" water of the mat is only weakly acidic (pH 6.4-6.5) and has a total alkalinity (titrated with H_2SO_4 to pH of 4.0) of 110 to 150 parts per million, calculated as $CaCO_3$.

The bog forest occupies the portion of the original lake basin peripheral to the sedge mat. *Larix laricina* (tamarack) forms a distinct forest girdle about 40 meters in width; young tamaracks adjoin the outer margin of the sedge mat, while the larger trees are farther back from the lake. Mosses and heaths are important as the ground cover in this area; *Cornus stolonifera* (red osier) and *Rhus Vernix* (poison sumach) are important shrubs. Since the tamaracks cannot reproduce in their own shade, *Thuja occidentalis* (white cedar) seedlings occur beneath the mature tamaracks; white cedars increase in size and importance peripheral to the tamaracks and dominate the major portion of the original lake basin. Towards the ancient shores occur scattered individuals of upland trees: *Pinus Strobus* (white pine) and *Betula lutea* (yellow birch) are common in local areas. Scattered seedlings and saplings of *Ulmus americana*



Cyclic changes in Cedar Bog Lake, 1931-1940. Fig. 4 (1931, photo by W. S. Cooper) shows lush growth of *Decodon* and high water level. Fig. 5 (1937, following several years of drouth) shows replacement of *Decodon* by *Typha* along the lake margin. Fig. 6 (1940) indicates partial recovery of *Decodon* following seasons of normal precipitation.

(elm), *Fraxinus nigra* (black ash) and *Acer rubrum* (red maple) indicate the trend of further succession.

Bottom Topography

The topography of the original lake bottom from the northwest to the southeast bog margin was determined by a series of borings to the sand substratum along the transect line shown in Fig. 3. Because of the great fluctuations in lake and bog levels during cycles of drouth and excess precipitation, as shown by the recent work of Buell (1941), it has seemed desirable to make all data dealing with depths of sediments conform to standard surface levels. The levels existing along the transect line on October 25, 1939, as surveyed with a Buff Level from upland bench marks, are arbitrarily taken as standards; all depths discussed in this paper are expressed in terms of these surface levels.

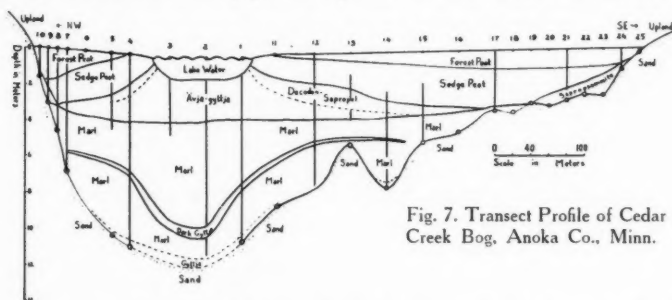


Fig. 7. Transect Profile of Cedar Creek Bog, Anoka Co., Minn.

The contour of the sand bottom along the transect line is shown in Fig. 7. The exact depth from the bog surface to the sandy substratum was determined for 21 of the 25 profile stations established, as indicated by small circles along the line representing bottom contour. It will be observed that the deepest portion of the original lake bottom is quite near the northwest margin. At station 2 in the center of the present lake, a modified Davis borer penetrated to a depth of 11.4 meters without reaching the substratum; the nature of the compacted sediments at this point indicated, however, that the underlying sand was not far below. The bottom slope from the northwest peat margin out to station 7 is $10\frac{1}{2}^\circ$ from horizontal, very steep for a sand basin lake. The slope from the southeast margin out to station 13, on the other hand, is very gentle, although its regularity is strikingly broken by a deep pit or trough at station 14. Northwestward from station 13 the depth increases rapidly.

The apparent influence of bottom topography on vegetational succession is noteworthy: invasion from the southeast margin has undoubtedly proceeded much more rapidly than from the opposite shore, as evidenced by the vast expanse of bog forest southeast of the present lake. This effect of topography gains significance when we realize that the prevailing wind direction is from the northwest, which would ordinarily inhibit invasion from the wind-exposed lake shore.

Sequence of Sediments

The types of sediments now occupying the lake basin, as determined largely by macroscopic examination, are represented graphically in Fig. 7. Samples of sediments have been taken at depth intervals of 20 centimeters from profile stations 1, 2, 3, 7, 8, 9 and 10, and at 50 centimeter intervals from such depth-zones of the remaining stations as are marked by solid vertical lines. Because detailed microscopic and chemical studies of the collected sediments have not yet been completed, the following must be considered as a preliminary discussion. Many types of quantitative analyses on large numbers of samples are necessary to justify a more detailed interpretation of the Cedar Bog "thanatocoenoses."*

The major groups of lake sediments fall into diagenic series corresponding more or less closely to the major lake types. Oligotrophic lake sediments are usually highly mineralized as the result of faunal activity and subsequent oxidation. Dystrophic lake sediments consist of a series of humified, allochthonous "lake peat" substances known as *dy* (pronounced "dü").

The organic sediments of eutrophic lakes usually consist (Naumann, 1921) of a diagenic group known as *gyttja* (pronounced "yittja"). These sediments are highly coprogenic, produced by action of the benthic fauna on the settled planktogenic detritus or *ävja*; oxidation is incomplete and usually followed by some reduction due to seasonal depletion of dissolved oxygen.

Organic sediments belonging to a diagenic series known as *sapropel* (sensu Lauterborn, 1901) sometimes occur in eutrophic waters. Sapropel is formed under stagnant anaerobic conditions which exclude animal life; heterotrophic bacteria initiate extensive reductive processes usually resulting in the emission of H_2S ; the resulting deposits are black and putrified. According to Wasmund (1930), sapropel may be found in (1) deep pockets in the bottoms of eutrophic lakes, (2) very small oligohumic waters, (3) waters with excessive sewage pollution, (4) waters with gypsum substrata, (5) waters with extended winter anaerobiosis, and (6) brackish strand lakes and stagnated lagoons. Sapropel in shallow waters is largely derived from the cellulose-rich detritus of higher plants, or *förna*.

It must be emphasized that the above sediments do not always appear as pure "genotypes," and that a certain amount of variation and intergradation must be expected. Some of the varieties and fasciations of these primary series have been described by Lundquist (1927), Naumann (1929) and Wasmund (1930). The sediment properties given above are somewhat categorical, based upon the published accounts of these European workers. Infallible methods of differentiation, applicable to American deposits in general, have yet to be developed; it is therefore highly desirable that careful studies be initiated to provide more precise chemical, physiological and biological criteria. Because English terms such as "mud," "muck," "slime," "ooze," and "sludge" are non-specific and confusing (Deevey, 1939, p. 700), the author urges critical

* A term introduced by Wasmund (1926) to include the semi-fossilized deposits of former biocoenoses.

examination and tentative recognition of the internationalized terms described in this paper.

Present information indicates that the earliest sediments in the profundal region (> 7 meters in depth) consisted of a thin deposit of silty *gyttja*, followed by a layer of fine-detritus *gyttja*. These same deposits are found in the "pit" beneath station 14, at a depth of 8 meters. The absence of mineralized autochthonous material in these early deposits is taken to indicate that "oligotrophy," usually considered as the pioneer stage of lake succession, was very transitory or absent.

The profundal *gyttja* deposit in the Cedar Bog Lake is of the dark brown type for a very brief distance, above which it gradually becomes grayish in color due to an increasing content of marl; this gray deposit is accordingly known as *marl-gyttja*. The marl content rapidly increases upward in the sediments until light gray marl forms a distinctive layer even at a depth of 10 meters below the present lake surface.

Vertical continuity of the marl is broken by the interposition of a sharply defined *gyttja* layer. This thin dark brown stratum has been encountered in every profile series penetrating more than 6 meters of sediment, but no evidence of it has been found in the shallower marginal profiles. Although no pollen chronology of the sediments has yet been made, this stratum appears to represent the deposit of a period during which the ecological status of the lake must have been profoundly altered. The conditions giving rise to this remarkable deposit are as yet unknown.

Above this distinctive *gyttja* stratus the deposits undergo a rapid reversion through *marl-gyttja* back to marl. In those marginal areas 4 to 6 meters in depth marl is the earliest sediment, being deposited directly upon the sandy substratum. Marl almost uniformly covers all earlier deposits up to a level about 4 meters below the present surface. The absence of marl above this level is as yet unexplained.

The great abundance of marl in the Cedar Bog deposits, constituting about 50% of the total sediment, can only be explained as a result of the drainage into the lake basin of calcium and magnesium ions from the surrounding upland. Thiel (1930) pointed out that marl is usually the earliest autochthonous deposit in lake basins of the Anoka Sand Plain. Although the outwash sand surrounding the Cedar Bog is not high in calcareous substances, intense leaching has removed much of the alkaline-earth content from this loose-textured porous soil. Also, the movement of sluggish streams of water through the inlets to the lake must have contributed greatly to the calcium and magnesium supply.

In the deeper portion of the marl deposit the carbonate is compacted and in very minute particles; in the upper region of the deposit the marl occurs in coarse flakes, together with an abundance of snail shells and pondweed seeds which clearly indicate its biotic origin. Between these carbonate flakes is found a matrix of brownish organic ooze which rapidly increases upwards in proportion to the marl content. Above the 4 meter level this organic ooze occupies

the remaining space between the marl and the present open water zone. The present lake is actively increasing the amount of this deposit at such a rapid rate that the open water area will doubtless be completely filled within a relatively short time.

This sediment, derived largely from pondweeds, epiphytic *Gloeotrichia* and blue-green phytoplankters, may be described as follows: consistency practically liquid, 97% water; coprogenic, the particles composed almost entirely of fecal balls from chironomid larvae; color brownish-gray; odor very slight, "marshy" rather than sulphurous; pH near 7.0; total alkalinity 200-1000 ppm as CaCO_3 ; soluble iron up to 20 ppm; ciliate protozoan fauna very abundant; coarse detritus (retained by sieve 40 meshes per inch) 5-10%; little diagenesis apparent in 3 meters of depth. According to the criteria given by Wasmund (1930) this deposit belongs to the *ävja*→*gyttja* diagenic series. For want of a more specific term the sediments beneath the present lake are correspondingly termed *ävja-gyttja*.

Near the margins of the present lake the bottom sediments are blacker, firmer, less coprogenic and more strongly reduced. Decomposing materials from the marginal *Decodon* as well as from other parts of the sedge mat are mixed with the aquatic constituents, adding to the coarse detritus content. The above characteristics indicate that the lake sediments in this area should be classified with the *sapropel* series. The sediments of the intermediate area represent transitional phases between these two types. Beneath the sedge mat and adjacent portions of the bog forest the *ävja-gyttja* becomes mixed with and finally gives way to a black *sapropel* deposit containing much coarse detritus, composed largely of *Decodon* fragments. This deposit is accordingly termed *Decodon-sapropel*.*

One further aquatic sediment should be mentioned. The shallow littoral areas of the original lake, shown at each end of the transect, are covered by a sandy organic sediment with distinctive properties. This littoral deposit consists largely of the blackened, semi-bituminized fragments of leaves, twigs and other substances presumably washed into the lake from the adjacent upland or washed into "drift piles" near the shore by wind action. Fine sand, diminishing in quantity upwards, occurs throughout this sediment, which is tentatively labeled *sapropsammite* for the southeast shore shown in Fig. 7, while the corresponding sediment near the northwest-shore occupies a space too small to be labeled. Wasmund (1930, pp. 345-347) discusses littoral deposits of this type as possible precursors of petroleum-bearing sands. In the Cedar Bog a sharp transition line separates this sediment from over-lying sedge peat.

* Such an effect of the marginal vegetation on the lake sediments is most unusual for a northern bog lake. Bog lakes in this latitude are usually surrounded by acidic sedge mats dominated by *Chamaedaphne* and *Sphagnum*. The contribution of such marginal vegetation to the bog lake sediments is usually in the form of flocculent, light brown *dy*, and such lakes are accordingly termed dystrophic. Cedar Bog Lake is definitely not dystrophic.

Beneath the sedge mat and peripheral areas the sapropel layer can be sharply differentiated from the superimposed *sedge peat*, formed by the roots and rhizomes of the sedge mat vegetation. As this layer is continuously augmented by fresh deposition it becomes heavier and tends to "squeeze" the more tenuous gyttja and sapropel over which the sedge mat has been floating, so that finally these sediments become compressed into strata only a fraction of their original depth, much of the space which they originally occupied having been replaced by sedge peat. This vertical pressure may also have had a horizontal component, tending to increase the amount of tenuous gyttja beneath the open water area.

Metabolism of the vast bog forest community encircling the sedge mat forms humus materials which accumulate beneath the trees and finally form a thin layer known as *forest peat*. In the sediment-profile (Fig. 7) forest peat covers the sedge peat under the area occupied by the bog forest.

Summary

The Cedar Creek Bog was formed as an ice-block lake in pitted sand-outwash topography, following recession of Keewatin ice during the Late Wisconsin glaciation. The lake is at present in a late stage of senescence, water occupying less than $\frac{1}{10}$ of its original depth and area.

Marginal succession is proceeding with great rapidity; the sedge mat vegetation showed radial invasion of 0.95 meter in 5 years. Nine years of observations, supported by photographic evidence, indicates that precipitation has been an important factor in the dominance of *Decodon* over *Typha* as the foremost invader of the encircling sedge mat. An extensive forest of *Thuja occidentalis*, encompassing a girdle of *Larix laricina*, covers the peripheral area of the lake basin.

Observations on the sediments of the Cedar Bog basin indicate that *marl* is the most extensive deposit, comprising at least 50% of the total. The marl is underlain in the deepest areas by a thin layer of *fine-detritus gyttja*, and is interrupted in its middle region by a second thin, sharply marked stratum of gyttja. The marl ceases abruptly above a sediment depth of 4 meters. A silty deposit tentatively termed *sapropsammite* occurs in the littoral area of the lake basin at sediment depths of 1 to 3 meters. The present lake is underlain by a deposit described as *avja-gyttja*, which merges peripherally into a blackish type designated as *Decodon-sapropel*. Beneath and peripheral to the sedges mat occurs a thick layer of *sedge peat*, overlain beneath the bog forest by a thin stratum of *forest peat*.

REFERENCES

1. BUELL, M. F. AND H. F. BUELL. 1941—Surface Level Fluctuations in Cedar Creek Bog, Minnesota. *Ecology* 22(3). In press.
2. COOPER, W. S. 1935—The history of the Upper Mississippi River in Late Wisconsin and postglacial time. *Minnesota Geol. Survey Bull.* 26:1-116.

3. DEEVEY, E. S. 1939—Studies on Connecticut lake sediments. I. A postglacial climatic chronology for southern New England. *Amer. Jour. Sci.* **237**: 691-724.
4. LAUTERBORN, R. 1901—Die sapropelische Lebewelt. *Zool. Anz.* **24**:50-55.
5. LEVERETT, F. AND F. W. SARDESON. 1932—Quaternary Geology of Minnesota and parts of adjacent states. U. S. Geol. Survey Prof. Paper **161**:1-149.
6. LUNDQUIST, G. 1927—Bodenablagerungen und Entwicklungstypen der Seen. *Die Binnengewässer* **2**:124 pp.
7. NAUMANN, E. 1929—Einführung in die Bodenkunde der Seen. *Die Binnengewässer* **9**:126 pp.
8. SMITH, W. G., G. H. NESOM AND E. G. ROTH. 1916—Soil survey of Anoka Co., Minnesota. U. S. Bur. Chem. & Soils **1916**:1807-1832.
9. THIEL, G. 1930—The marls of Minnesota. *Minnesota Geological Survey Bulletin* **23**:79-193.
10. THWAITES, F. T. 1935—Outline of glacial geology. Edwards Bros., Ann Arbor, Mich., 115 pp.
11. WASMUND, E. 1926—Biocoenose und Thanatocoenose. *Arch. Hydrobiol.* **17**:1-116.
12. ————1930—Bitumen, Sapropel und Gytja. *Förh. Geol. Fören. Stockholm* **52**:315-350.

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Distribution of Birds in Relation to Major Biotic Communities¹

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Introduction

Zoogeographical and ecological study of North American avifauna is of recent development. Aside from Allen's early distributional sketch (1871), active investigation in this field did not come until the early 1890's, when the U. S. Biological Survey began to study mammal and bird distribution in various parts of the North American continent to ascertain the 'life-zone' relationships of this distribution. Likewise, aside from Adams' early discussion of community succession (1909), application of the concepts of modern ecology to local distribution of avifauna has become active only within the last decade.

Modern ecologists have pointed out failings of the life-zone concepts, but these criticisms have not been accompanied by any attempt to bring together material of interest to the ornithologist and to apply to it the concepts of ecology. The present report, necessarily limited in scope, is a preliminary consideration of this problem. Essentially, this has involved (1) an accumulation of distributional data on a number of species, (2) the mapping of the extent of their ranges on the basis of these data, and (3) the analysis of each range together with known habits of the species in relation to major biotic communities.

Life Zones and Life-Zone Criticisms

The life-zone concept was developed in a study under the leadership of Dr. C. Hart Merriam of the zonal distribution of birds and mammals in the San Francisco Mountains of Arizona (1890). The results of this investigation together with an examination of distributional data on North American birds and mammals led him, in 1894, to the formulation of a principle of plant and animal distribution based on temperature summations and their isotherms. A general agreement between the range limits of various birds and mammals and these isotherms convinced him that this temperature factor was the critical one in distribution.

This concept was, therefore, based on two sets of data: (1) the actual facts of distribution and (2) the causal factors, stressing temperature. A general analysis of these is not within the scope of the present work; suffice it to indicate that from the experimental side, the latter have been criticized by Livingston and Shreve (1921), Kendeigh (1932), and Shelford (1932). More recently, Daubenmire (1938) has summarized these criticisms together with others of lesser import.

¹ Contribution No. 562 from the Zoological Laboratory of the University of Illinois.

However, aside from the difficulties of the temperature theory, the zonal distribution and agreement of range limits still remain to be examined. From this faunistic aspect, Ruthven (1920) and Dice (1923) have pointed out in the case of all terrestrial vertebrates except birds that with few exceptions correlation of species with life zones is negligible. In bird distribution these zones have been used chiefly to distinguish groups of associating species, implying an ecological significance. That they are not ecological units has been shown by Dice (1923) and Shelford (1932), and we are, therefore, left to examine the significance of the avian life-zone associations which are stressed by most ornithologists in any discussion of bird distribution. This is taken up here from the ecological point of view rather than the zoogeographical; any conclusions apply only to the ecological aspects of the life-zone concept.

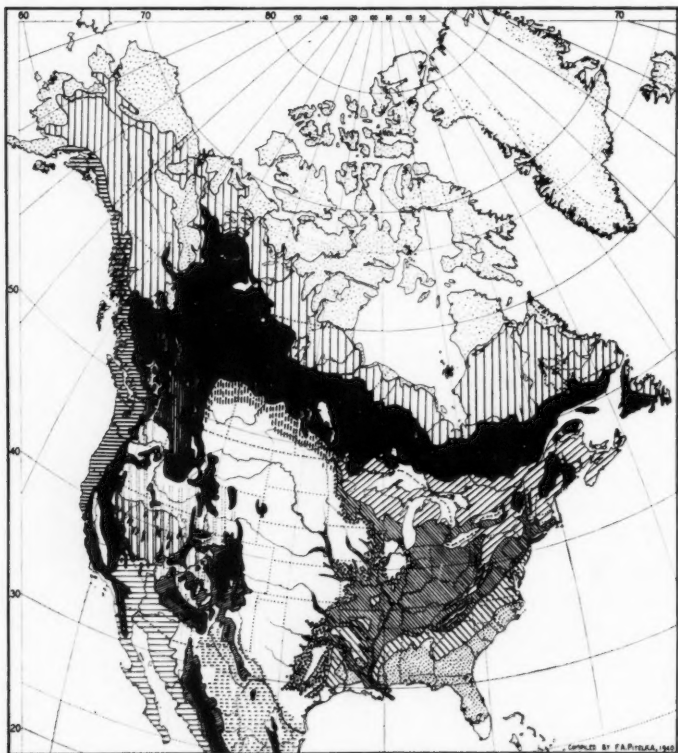


Fig. 1. Major biotic communities of North America showing extensive ecotones and subclimaxes. See key on opposite page.

Biomes

Modern ecologists today recognize the natural unity of such landscape aspects as tundra, coniferous forest, deciduous forest, etc. (See Fig. 1). These units are entities both florally and faunally, and each exemplifies the basic and largest unit of biotic communities. Such a unit is termed a *biome*. This concept has been advanced chiefly by Clements and Shelford (1939) in both fields of animal and plant ecology, and the system of community classification which they propose, of equal value to both plant and animal ecologists, has worthwhile application in ecological studies of birds. (See also Carpenter, 1939).

In terrestrial biomes, with which we are here concerned, vegetation constitutes the *dominant* or controlling element of the community, while animals, in general, are community constituents exerting an effect on the community in varying degrees, depending chiefly on their abundance, size, and habits. Though such easily recognized natural areas as North American grassland and deciduous forest are biomes, it should be pointed out that this community unit includes not only the vegetation of a characteristic life-form, but also all other vegetation of a developmental or subordinate nature. There is in every natural region a definite order of communities which successively occupy original or secondarily formed bare area. This series of communities is termed a *serie*; the earlier developmental communities in the succession are *seral*, the later ones are *subclimax* communities, and the last community of such a succession is the *climax* which is self-perpetuating and is characterized by a life-form of the dominants, such as grass, deciduous forest, etc. The dominants of developmental stages within a climax region may or may not be of the same life form, as, for example, seral stages in the deciduous forest climax may include herbs, grasses, shrubs, and both coniferous and deciduous trees. The distributional control of biomes is, broadly speaking, climatic, and their limits are recognized by the occurrence

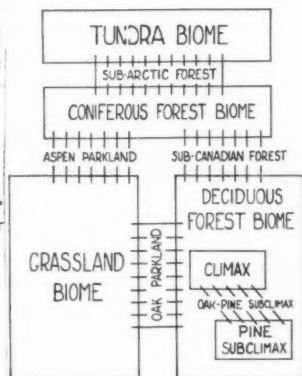
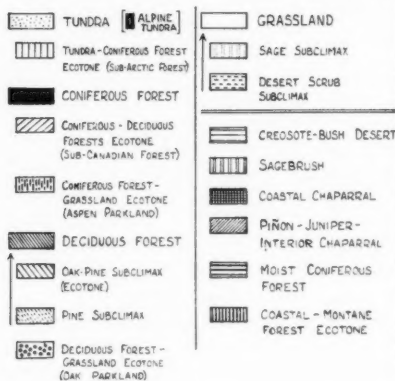


Fig. 2. Diagrammatic representation of the relationship of North American biomes and their ecotones east of the Rocky Mountains.

of the climax associations of dominants. The climax may be interrupted locally in the presence of some different group of dominants really subclimax, but more stable than the usual subclimax communities due to a particular condition of soil or topography.

Our knowledge of North American biomes, as such, is perhaps most extensive, though still in many ways fragmentary, on the grassland, coniferous forest, deciduous forest, and tundra. They are the largest such ecological units and occur in extensive masses with broad *ecotones* (transitional areas) in temperate North America east of the Rocky Mountain range. Their relationship is shown diagrammatically in Fig. 2. This diagram has been included further for the purpose of indicating and emphasizing the subordinate relationship of the ecotones to the climaxes, and this should be kept in mind when one studies the map showing the major biotic communities of North America. Extensive ecotones and subclimaxes are included since their regional nature and intermixture or differentiation of life forms which occur within them is of importance in bird distribution. The map is based on the phyto-distributional works of Shelford (1926), Shantz and Zon (1927), Bird (1930), Nichols (1935), Brand (1936), Mattoon (1937), Halliday (1937), Weaver and Clements (1938), and Muller (1939).

The major communities of the west and southwest are indicated on an equal basis with the four biomes treated above. The former include the moist coniferous forest, sagebrush desert, coastal chaparral, pinyon-juniper and interior chaparral (combined on the map), and creosote-bush desert. While these are recognized as plant formations by Weaver and Clements (1938), sufficient study of a bio-ecological nature has not been done to justify their designation as biomes.

Designation of Birds' Ranges

Up to the present, such authoritative works as the A. O. U. Check-List (1931) and the life-history collections of Bent (e.g., 1932) give statements of ranges in which the outer posts of occurrence are cited, though records of an accidental or casual nature are eliminated as much as possible. However, if these outer posts of occurrence are plotted on a map and a line connecting them is drawn, the result is a breeding-range designation that is often inadequate and sometimes incorrect due to its inclusion of areas within which the species is irregular or even not known to occur. Such a designation disregards ecological distribution of the community of which the species is a member and it further disregards the more important problem of relative abundance and, therefore, relative importance of a species within the various parts of its breeding range (Grinnell, 1927; Clements and Shelford, 1939).

As regards the ecological approach, these points cannot be overemphasized since the prevalent disregard for the importance of relative abundance of species within a range is a deterrent to an understanding of bird distribution as a phenomenon related to communities. While correlation between bird ranges and biomes appears to be confined largely to species characteristic of climax

communities, at the same time such correlation may occur in the varying abundance of a species spreading over several biomes, thereby providing evidence as to the exact nature of their community relations and the factors governing their distribution.

Methods

The attempt to show correlation of birds' ranges with major communities has been considered from two points of view. First, the species of a taxonomic group were tested for biome correlation, using the family Tetraonidae (North American grouse). The group is a well-distributed one and is represented by one or more species in almost all of temperate and arctic North America; furthermore, the size, habits, and abundance of grouse make them an ecologically important group in those regions not dominated too much by man. Second, eleven species associated with the deciduous forest in north-central states were tested for biome correlation; four species from the coniferous forest are added for illustrative purposes. Time and space limitations did not permit the expansion of this investigation to include more species, but we hope later to make a more extensive application of these principles.

To obtain as much detailed information as possible on local distribution, abundance, and habitat relationships of these species, over 200 local and regional studies of avifaunal distribution were consulted. The problem of abundance within the breeding range could be considered only for ten species found in the deciduous forest, the region where local data are most voluminous. The remaining species are treated only from the distributional and niche-relationship angles.

Distributional lists make use of various terms such as 'abundant,' 'fairly common,' 'tolerably common,' 'rather uncommon,' etc., to indicate relative abundance of species. The quasi-quantitative nature of these and the varied meaning which the combinations may have in the minds of different ornithologists made it necessary to reduce all such designations to one of three, namely, common, uncommon, and rare. These words, as used here, imply degrees of abundance, which so far as an individual species is concerned, serve adequately for diagrammatic differentiation on a map. But in comparing species, these are to be interpreted more accurately as degrees of frequency; that is, red-eyed vireos may be more numerous in a given tract of woods than scarlet tanagers, which would lead one to think that the vireo should be designated as common, the tanager uncommon. But for that sample tract of woods as compared with other similar tracts, their frequency is practically the same. Thus, in the center of their ranges — the deciduous forest region — given the niche, the species are present. To restate for sake of clarity, on the map of a single species, 'common,' as against 'uncommon' and 'rare,' as regards portions of its range, indicates a degree of abundance; among several species, 'common,' comparatively speaking, indicates a degree of frequency, since 'common' as a degree of abundance cannot apply equivalently to all the species.

During the accumulation of distribution and abundance data, a master map was kept for each species, and a selection of colors was used to indicate simple occurrence or degree of abundance. For local areas, dots were placed on the map to indicate common, uncommon, or rare; for larger areas, as states, the

entire area was shaded according to the summarization of occurrence within the entire area. The final accumulation of dots and shadings scattered throughout the range of the species permitted the drawing of fairly accurate range limits and differentiation within this range into the three degrees of occurrence. Where specific information was given as to particular communities within which the species was abundant, as for instance, the scarlet tanager along stream-side woodland in the prairie states, an attempt was made to embody this fact into the map to show more accurately actual distribution and to better present the possible relations of the entire range to major communities.

Upon first glance, the maps indicating abundance may be thought to show an obviously erroneous evenness of distribution. However, these actually show (1) abundance within the niche or the particular vegetational type inhabited by the species concerned²; or (2) availability of the niche itself so that the particular vegetational type supports its characteristic avifauna, the distribution of which corresponds to the regional segregation of that vegetational type and its peripheral gradient of diminishing abundance. This becomes evident from a study and comparison of vegetation and bird-distribution maps.

In the following sections, each of the 27 species is taken up individually in

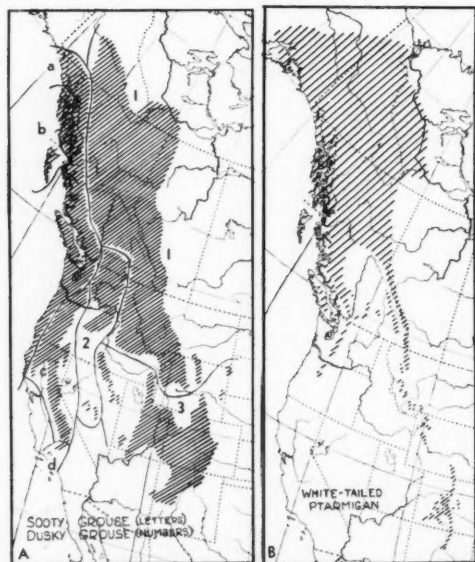


Fig. 3 (A) Range of *Dendragapus fuliginosus* (a) *fuliginosus*, (b) *silkensis*, (c) *sierrae*, (d) *howardi*; and *Dendragapus obscurus* (1) *richardsoni*, (2) *pallidus* (Swarth, 1931), (3) *obscurus*. (B) Range of *Lagopus leucurus*.

² See footnote page 131.

a manner suggestive of a much-needed 'ecological check-list' of birds. Niche relationships are considered briefly together with the circumstances of correlation of the ranges with relation to major communities. In many of the grouse, certain habits which involve the movements of the species from one community into another necessitates the mention of these in a treatment of general community relations.

A map accompanies the treatment of each species. Two general types are included — simple distribution maps and abundance maps — and the reader is asked to read each figure explanation in order not to confuse methods of designation. Unless otherwise indicated, taxonomic designations follow the A. O. U. Check-List (1931); exceptions to this are accompanied by references listed in the figure explanation under each map.

Ecological Classification of North American Tetraonidae

A. CONIFEROUS FOREST SPECIES

1. *Dendragus fuliginosus*. The scoty grouse ranges through most of the moist coastal belt forest and extends southward in the Sierran montane forest (Fig. 3), inhabiting coniferous forests from sea coast to subalpine zones of the highest mountains. These grouse confine themselves to the dense fir, cedar, and hemlock growths during the winter, but move into subclimax, even semi-open thickets, where greater food supply is available, to nest, returning to the coniferous forest only to roost and to seek shelter from enemies.

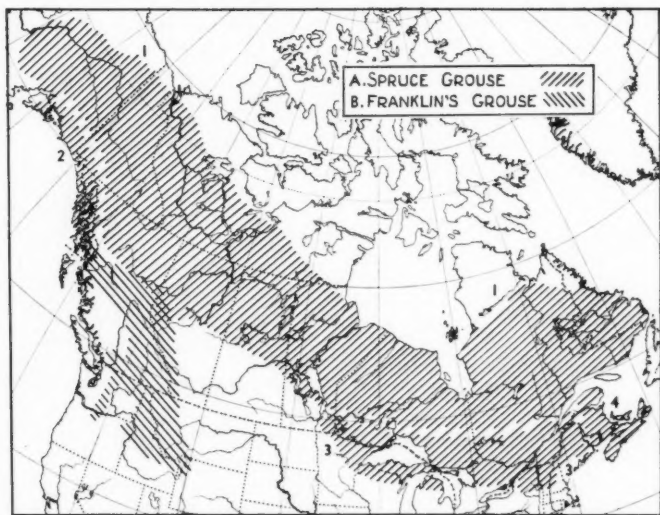


Fig. 4. Range of (A) *Canachites canadensis* (1) *canadensis*, (2) *atratus*, (3) *canace*, (4) *torridus* (Uttal, 1939); and (B) *Canachites franklini*. Areas of subspecific intergradation are shown by bands formed by broken alternate lines.

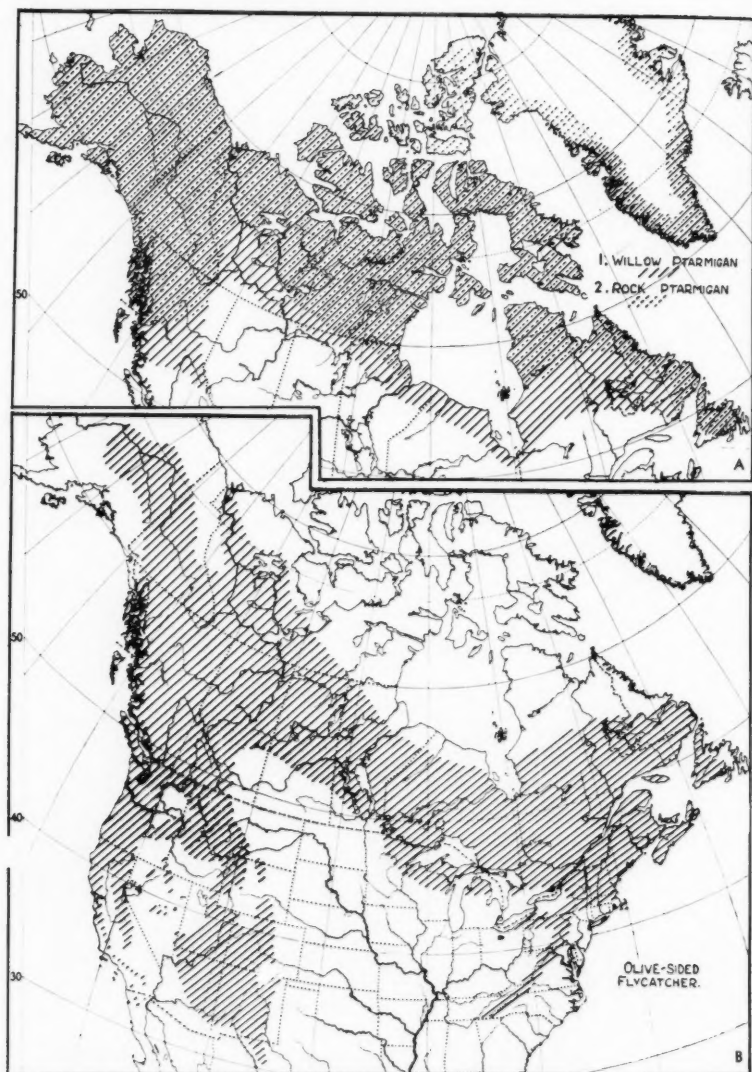


Fig. 5. (A) Range of (1) *Lagopus lagopus* and (2) *Lagopus mulus* (Peters, 1934).
(B) Range of *Nuttallornis mesoleucus*.

2. *Dendragapus obscurus*. The dusky grouse ranges throughout the petran montane forest (Weaver and Clements, 1938, 481) north of central New Mexico and northern Arizona (Fig. 3). The species is characteristically a bird of the dense coniferous forest growths within which it will nest, but like *D. fuliginosus*, moves down the mountain sides to breed in thickets and forest-edge situations of the upper foothills and also upward into subalpine, open areas.

3. *Canachites canadensis*. The spruce grouse is characteristic of the trans-continental belt of coniferous forest (Fig. 4), occupying the ecotones to the tundra and, formerly, to the deciduous forest. Though non-migratory, regular local movement takes place during late summer in response to abundance of food outside of their characteristic habitat, chiefly into semi-open subclimax areas.

4. *Canachites franklini*. The community relations of the Franklin's grouse are similar to those of the spruce grouse. It occurs in the northern portion of the petran montane forest (Fig. 4), and like *C. canadensis* occupies a short portion of the coastal belt forest below that occupied by the latter species.

B. TUNDRA SPECIES

1. *Lagopus lagopus*. The willow ptarmigan is a bird of the arctic tundra and sub-arctic forest (tundra-coniferous forest ecotone) (Fig. 5). It is confined to well-developed areas of tundra and to the alder, willow, and stunted spruce growths. The species is resident and any spring or fall movements can be correlated with food supply (Bent, 1932). (See also *L. leucurus*).

2. *Lagopus mutus*. The rock ptarmigan occupies a range somewhat similar to that of *L. lagopus* but avoids the sub-arctic forest and ranges further north (Fig. 5). It is a bird of rocky and barren, unvegetated grounds — early seral stages — as against the niche occupied by *L. lagopus*, the climax tundra and postclimax³ forest growths. Where the two species occur together, their ranges more or less "interdigitate."

3. *Lagopus leucurus*. The white-tailed ptarmigan inhabits the alpine meadows and the open, rocky summits of the Rocky Mountains and northern Sierras from northern New Mexico and Oregon northward (Fig. 3).

Since the North American tundra is divided into three associations (Weaver and Clements, 1938), the numerous races of *lagopus*, *mutus*, and *leucurus* appear non-significant in ecological distribution. The variation is local, irregular, and in most cases so slight (Bent, 1932, 202), that taxonomists dispute each other's determinations of the races, and very likely this variation is more a matter of local isolation in a resident species rather than the expression of some environmental difference.

The ptarmigan group, like the blue-grouse group (*Dendragapus* and *Canachites*) occupies one entire biome, and where two or three species occur,

³ Postclimax — refers to relict communities persisting in a present-day climax from previous moister periods.

as in northern British Columbia and Yukon, they occupy different niches, *lagopus* remaining in the lower, well-developed tundra, *mutus* in the barren, rocky areas, and *leucurus* in the higher portions of the northern Rockies. In parts of Alaska where *leucurus* does not occur, *mutus* also occurs in the mountainous regions.

C. GRASSLAND SPECIES

1. *Tympanuchus cupido*. Formerly, the prairie chicken was confined to the tall grassland associations of the prairie biome (Fig. 6B). Previous to 1872,

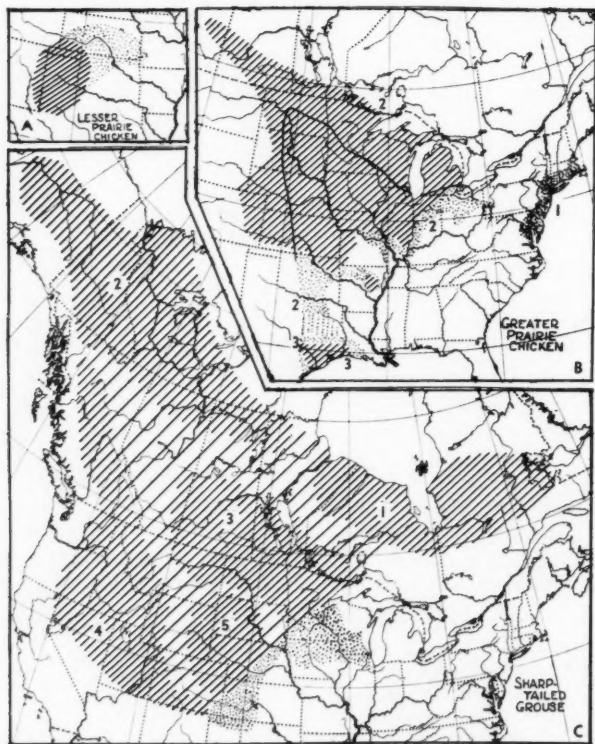


Fig. 6. (A) Range of *Tympanuchus pallidicinctus*. (see note below). (B) Range of *Tympanuchus cupido* (1) *cupido*, (2) *pinnatus* (Peters, 1934), and (3) *altwaleri*. Former limits of westward and northward distribution of *T. c. pinnatus* shown by line within present range. (C) Range of *Pedioecetes phasianellus* (1) *phasianellus*, (2) *hennicolti*, (3) *campestris*, (4) *columbianus*, and (5) *jamesi* (Snyder, 1939). Note: Areas of subspecific intergradation are indicated by bands of sparser lining; areas of former occurrence are shown by dotting.

the species did not occur in northwestern Minnesota or northern Dakota, but has since then invaded cleared lands of the southern Canadian provinces in the region of the aspen parkland, where it has replaced the forest-edge species, *Pedioecetes phasianellus*.

T. c. pinnatus occupies the true prairie and prairie peninsula while *T. c. altwateri* is the coastal prairie form. *T. c. cupido* formerly occupied the coastal barrens of the New England and middle Atlantic states. The relationships of *pinnatus* and *cupido* and the past occurrence of the former race into the eastern reaches of the prairie peninsula provide an example from the class Aves for support of the hypothesis of a postglacial eastward extension of the North American grassland discussed recently by Schmidt (1938).

2. *Tympanuchus pallidicinctus*. The lesser prairie chicken inhabits the short-grass prairie in the lower Great Plains region within the United States (Fig. 6-A). It is particularly restricted to a portion of the American grassland north

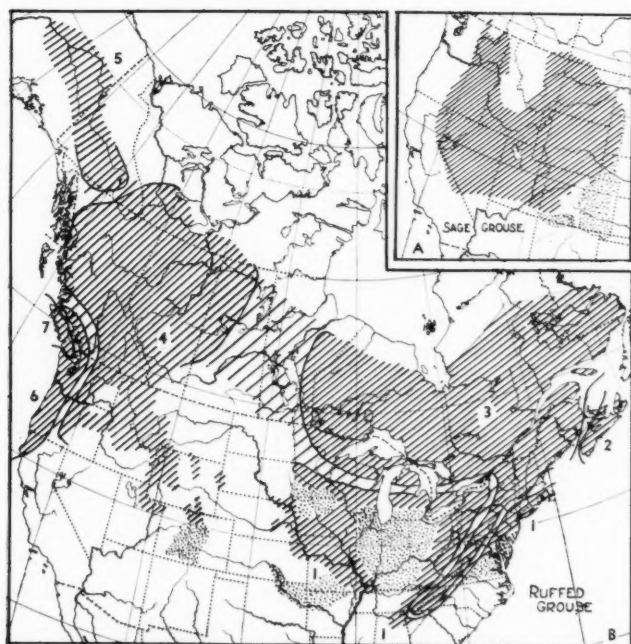


Fig. 7. (A) Range of *Centrocercus urophasianus*. (B) Range of *Bonasa umbellus* (1) *umbellus*, (2) *thayeri*, (3) *togata*, (4) *umbelloides*, (5) *yukonensis*, (6) *sabini*, and (7) *brunnescens* (Conover, 1935). Areas of subspecific intergradation and former occurrence are shown as in Figs. 4 and 6.

of the Rio Grande unoccupied by either of the other two grassland forms, i.e., *Tympanuchus cupido* and *Centrocercus urophasianus*.

3. *Centrocercus urophasianus*. The sage grouse is found in the arid plains of the western United States and extreme southern Canada (Fig. 7-A), occupying the basin sagebrush, the Palouse prairie (Clements and Shelford, 1939, 290), and the western portions of the short-grass prairie; within the last two grassland communities, sage (*Artemisia tridentata*) is a subclimax shrub, though some question exists whether it is climax even in the Great Basin, where bunch grass is intermixed with sage in the most advanced growths. While the range of the sage grouse is coextensive with sage, the problem of its range delimitations doubtlessly involves other factors, one of which may be the niche-relationship of grassland Tetraonidae mentioned under *Tympanuchus pallidicinctus*.

D. SPECIES OF TEMPERATE FOREST PARKLANDS AND DECIDUOUS AND CONIFEROUS FOREST SUBCLIMAXES

1. *Bonasa umbellus*. The ruffed grouse is throughout its range (Fig. 7-B) a bird of subclimax situations — forest openings, second growth — where a mixed habitat of brush and trees is available, and is seldom encountered in climax stands of deciduous or coniferous forests. Like the other Tetraonidae, this species exhibits the habit of local movements in response to abundant food supply.

2. *Pedioecetes phasianellus*. The sharp-tailed grouse is a species of brush lands and open areas in forests within the sub-arctic and coniferous forests and adjacent to temperate grasslands (Fig. 6-C). The ruffed grouse, though having a similar range, requires denser thickets and woods and includes the deciduous forest region in its range. In areas opened partially by cultivation, the sharp-tail invades and frequents fields where abundant food is available, but as cultivation becomes more intensive and the land is denuded of thickets and scattered forest growth, the species disappears. In the parkland region of the prairies west of the Mississippi and in northern Illinois, the sharp-tail disappeared with the removal of scattered deciduous forest groves, where it was formerly known as the 'bur-oak grouse,' while in the southern parts of the Canadian provinces of Alberta and Manitoba, the clearing of lands caused a recession of *P. phasianellus* followed by an invasion of the prairie chicken, *Tympanuchus cupido* (Bent, 1932, 291).

Deciduous Forest Species

1. *Antrostomus vociferus*. The whip-poor-will, while generally associated with deciduous forest, is not characteristic of the climax associations; rather it is found in semi-wooded, dry, rolling uplands, forest edge, and second-growth thickets. Yet the race *A. v. vociferus* (Fig. 8-A) is confined to the deciduous forest biome with the exception of southern portions, where competition with the chuck-will's widow (*Antrostomus carolinensis*) may be a limiting factor in its distribution.

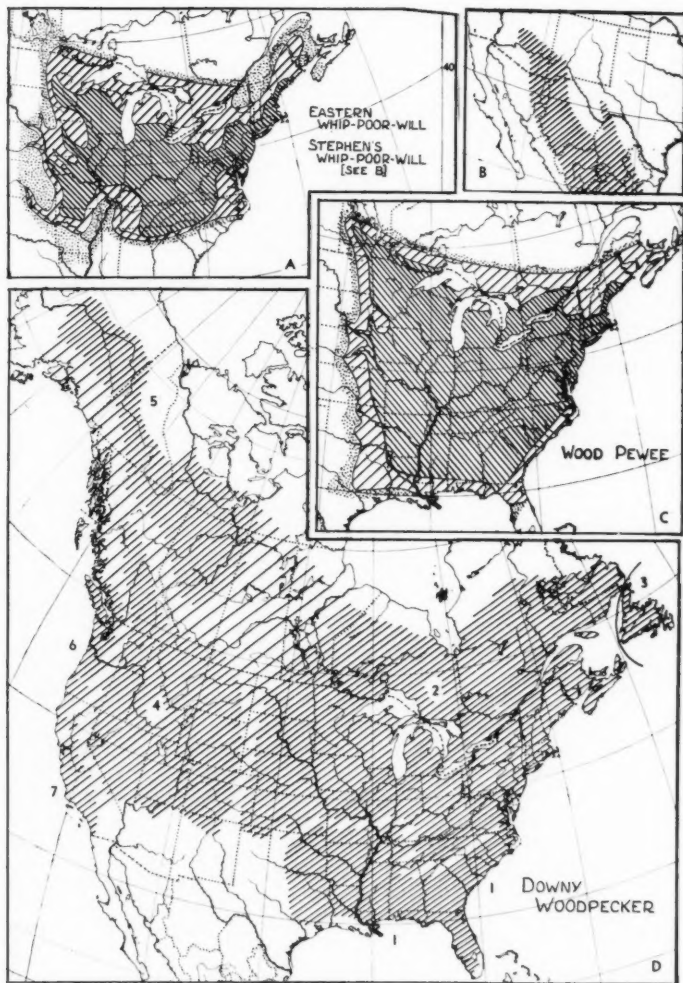


Fig. 8. (A) Range of *Antrostomus vociferus vociferus* broken into areas of common (central), uncommon, and rare (peripheral) occurrence. (B) Northern portion of range of *Antrostomus v. arizonae*, indicating extent of occurrence only. (C) Range of *Myiochanes virens*, showing areas of common, uncommon, and rare occurrence as in (A). (D) Range of *Dryobates pubescens* (1) *pubescens*, (2) *medianus*, (3) *microleucus* (Oberholser, 1914), (4) *leucurus*, (5) *nelsoni*, (6) *gairdneri*, (7) *turatii*. Only extent of occurrence and areas of subspecific intergradation are shown.

Additional races occur in the southwest and southward through Mexico. *A. v. arizonae* is found in montane and sub-montane growths of pine and mixed oak-pine. The circumstances of distribution in this species — the two disjoined populations — provide an interesting problem in biotic isolation as a factor in speciation and the evolution of niche-relationships.

2. *Dryobates pubescens*. The downy woodpecker is abundant in the decidu-

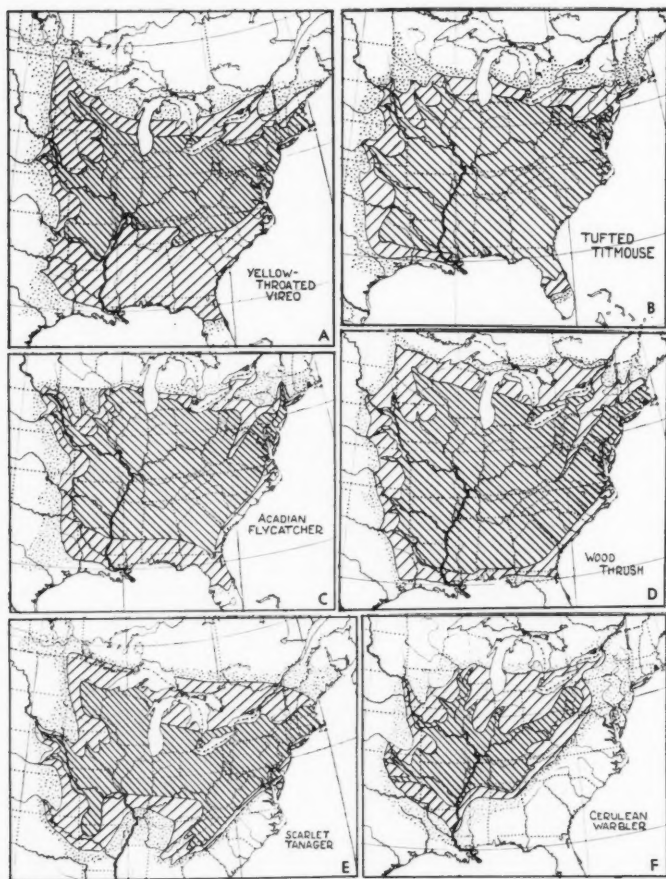


Fig. 9. Ranges of (A) *Vireo flavifrons*, (B) *Baeolophus bicolor*, (C) *Empidonax virescens*, (D) *Hylocichla mustelina*, (E) *Piranga erythromelas*, (F) *Dendroica cerulea*, showing areas of common (central), uncommon, and rare (peripheral) occurrence.

ous forest biome but occurs in *deciduous* growth over the whole of temperate North America (Fig. 8-D).

3. *Empidonax virescens*. The Acadian flycatcher, confined to the deciduous forest biome (Fig. 9-C), frequents undisturbed, well-watered forests chiefly along streams or in deep moist ravines.

4. *Myiochanes virens*. The wood pewee is a very characteristic and abundant species of the deciduous forest biome (Fig. 8-C), frequenting climax woodland as well as subclimax situations such as cedar swamps and forest edge and also orchards and extensive plantings of shade trees.

5. *Baeolophus bicolor*. The tufted titmouse is limited to the deciduous forest biome proper (Fig. 9-B), avoiding the sub-Canadian forest (deciduous forest-coniferous forest ecotone). It occurs in deciduous forest growths ranking from mid-seral to climax stages, most frequently, however, in mature floodplain forests.

6. *Hylocichla mustelina*. The wood thrush is confined to the deciduous forest biome (Fig. 9-D), frequenting chiefly climax and mature, well-drained floodplain forests.

7. *Vireo flavifrons*. The yellow-throated vireo is limited to the deciduous forest biome (Fig. 9-A), frequenting luxuriant bottomland forests and undisturbed upland climax forests.

8. *Vireo olivaceus*. The red-eyed vireo, perhaps the most abundant bird in the deciduous forest biome, spreads beyond the limits of this plant formation into the north and northwest where it occupies subclimax deciduous forest and mixed growths (Fig. 10-A). It is primarily a species of deciduous growth and occurs neither in pine flats of the southeast nor in the conifers of the north.

9. *Dendroica cerulea*. The cerulean warbler is a characteristic though somewhat restricted species of the deciduous forest (Fig. 9-A). It is confined to the undisturbed climax (upland) and subclimax (mature floodplain) forests.

10. *Seiurus aurocapillus*. In the deciduous forest biome, the oven-bird is a prominent species, frequenting climax and late subclimax forests and also mixed forests of deciduous and coniferous trees in the sub-Canadian ecotone (Fig. 10-B). However, in the coniferous forest portion of its range, it occupies a subclimax niche, frequenting poplar woods and mixed growths of deciduous trees and conifers.

11. *Piranga erythromelas*. The scarlet tanager is confined to the climax portions of the deciduous forest biome and to the sub-Canadian ecotone where a mixture of coniferous and deciduous climax occurs (Fig. 9-E). To the south, the species ranges only into mature upland deciduous forest and mixed oak-pine above the extensive areas of subclimax pines along the gulf and south Atlantic coasts.

Coniferous Forest Species

1. *Nuttallornis mesoleucus*. The olive-sided flycatcher is an excellent example of a coniferous-forest species, spreading over the entire continent, yet not

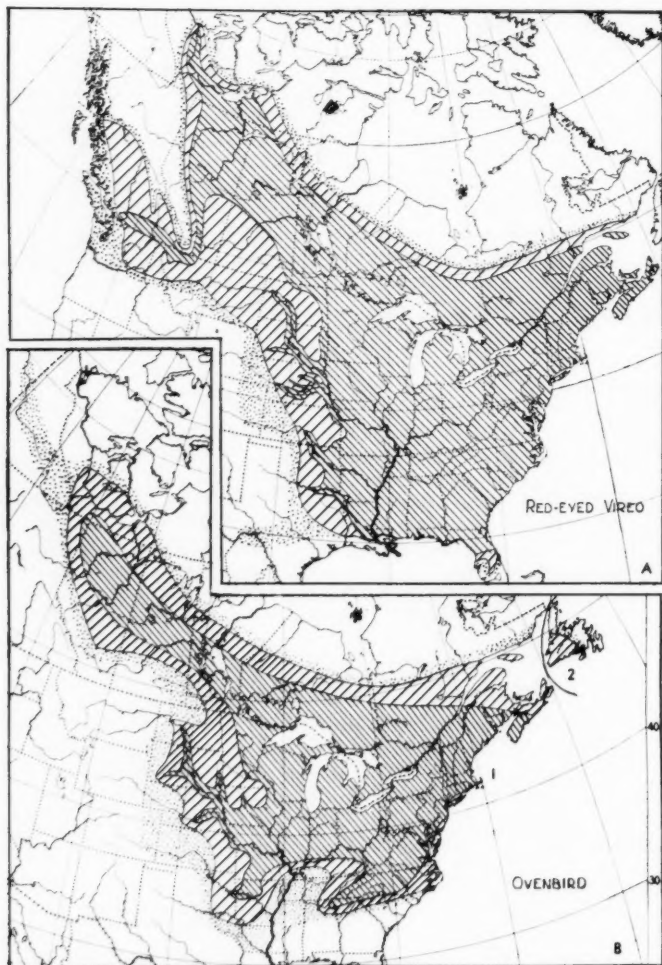


Fig. 10. Range of (A) *Vireo olivaceus* and (B) *Sciurus aurocapillus* (1) *aurocapillus* and (2) *furvior* (Batchelder, 1918), shown as in Fig. 9.

varying subspecifically to any appreciable extent (Fig. 5-B). Associated with coniferous growth, it is to be found from sea-level in the moist coniferous forest regions of the Pacific Coast up to short spruce timber at 11,000 feet in the Rockies.

2. *Empidonax flaviventris*. The yellow-bellied flycatcher is a characteristic species of dense coniferous growth, but also occurs in seral vegetation of second-growth birch or alder thickets. As in other species characteristic of dense coniferous growth, the extent of the range (Fig. 11-B) would suggest that to the north and northwest, the species is limited, in addition to other possible

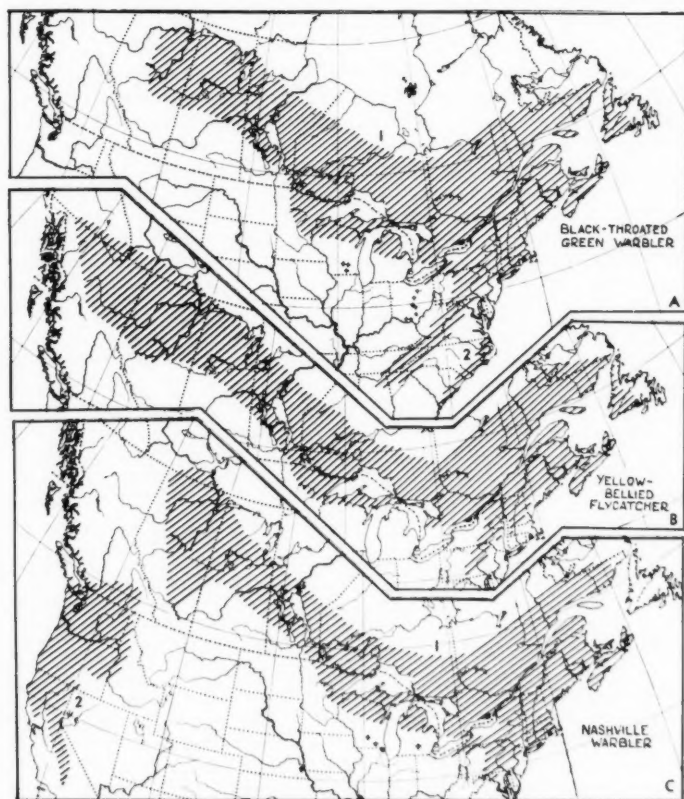


Fig. 11. Ranges of (A) *Dendroica virens* (1) *virens*, and (2) *waynei*; (B) *Empidonax flaviventris*; and (C) *Vermivora ruficapilla* (1) *ruficapilla* and (2) *ridgwayi*. Only extent of occurrence is shown. Small crosses indicate nesting records or local breeding areas outside of normal breeding range.

factors, by availability of suitable breeding situations inasmuch as in those regions, the coniferous forest proper becomes ecotonal in nature.

3. *Vermivora ruficapilla*. The Nashville warbler is a species of subclimax situations in the coniferous forest biome (Fig. 11-C) and its varied ecotones over the continent to the south or to lower levels in mountainous country. It frequents seral or subclimax vegetation in moist habitats as well as that on dry uplands.

Two races, *V. r. ruficapilla* and *V. r. ridgwayi*, are recognized. The community relations of the two appear to be comparable, and the circumstances of distribution with reference to the barrier afforded by the Rocky Mountains suggest the racial differentiation to be a result of geographic isolation.

4. *Dendroica virens*. The black-throated green warbler is a species of the coniferous forest biome (Fig. 11-A) and the coniferous forest-deciduous forest ecotone. It occurs chiefly in second-growth evergreens and in mixed forests of deciduous trees and conifers. To the south, the species occasionally, though infrequently, occurs in pure deciduous forest climax associations. In this connection, it is interesting to note that the race, *D. v. waynei*, is confined to the broad-leaved, mature swamp forests of the lower Atlantic coast. The diversity of vegetational relations as regards the two races and their isolation into separate breeding populations provides another excellent example for study of evolution of niche-relationships.

Discussion

In an acquaintance with animals, their behavior, habits, and distributional and ecological limitations, it soon becomes evident that no two species are identical in the sum total of environmental relations. However, granted that each animal is a unit physiologically and functionally, which makes it necessary to give the species special consideration, the fact that organisms do occur to the extent of intricate interrelations and interdependence makes a consideration of group behavior as important as individual behavior. Analyses of community compositions are studies of group behavior, and a phase of the same is the study of relation of species distribution to major communities.

The data as summarized above for 27 species of birds make several points apparent. Certain species agree well with the limits of biotic communities, as, for example, the ptarmigan in the tundra biome, the spruce grouse in the coniferous forest biome, the prairie chicken in the tall-grass associations of the grassland biome, and a series of passerines in the deciduous forest biome. This is particularly true of species confined to the climax associations within these biomes. On the other hand, there are species, as for example, the red-eyed vireo and ovenbird, which are abundant in the deciduous forest climax associations, but fall to a subclimax position (consistently inhabiting *deciduous* growth) in the coniferous forest portions of their ranges. Others, such as the ruffed grouse and sharp-tailed grouse, are characteristic of seral stages only and spread over several biomes.

Birds apparently do not respond to any specific differences among the dominant plants of a climax or any of its seral stages. Rather there are birds

of deciduous forest, coniferous forest, grassland, etc. More importantly, then, life-form, as a differentiating feature of a climax, seems to be a controlling factor in distribution. Any difference in life form of plants in different associations as, for example, the grassland associations of short grass, tall grass, or a mixture of two life forms as sage (a shrub) and bunch grass, may have an effect on niche relationships which would confine the species to one association or one life-form as the prairie chicken in tall-grass prairie. Likewise, extensive subclimaxes of different life forms, though within a biome as, for example, the southeastern pine subclimax, may have characteristic species not occurring in the deciduous forest climax, while the latter may have characteristic species which spread with it where it replaces the pine. Further, species characteristic only of subclimax vegetation — shrubs, small trees, forest edge — the life-forms of which or combinations thereof are found over several biomes, similarly range over several biomes. This is true of the sharp-tailed and ruffed grouse, while the downy woodpecker, a species inhabiting deciduous trees, spreads over temperate North America wherever these occur, be they climax or subclimax. Others, as the whip-poor-will, have discontinuous ranges as regards subspecies; they are not characteristic of a particular climax and, therefore, as is usually the case, not confined to a biome. Life-forms of early seral and mid-seral vegetation and combinations thereof are not limited to biomes; this would, of course, hold true also of vegetation of an ecotonal or transitional nature. The facts of bird distribution can be correlated well with these points.

Thus, geographic variation in which correlation with climatic differences is most evident occurs in those species ranging broadly over several biomes; e.g., the ruffed and sharp-tailed grouse, downy woodpecker, etc., among forms considered here, not to mention such well-known examples as the song sparrow (*Melodia melospiza*) and screech owl (*Otus asio*). Such forms are usually characterized of seral or subclimax stages—in any case, they are not confined to one climax. However, within larger, major communities (as tundra), variation may be effected more extensively through biotic and geographic factors, e.g., population behavior in the genus *Lagopus*. The secondary importance of macroclimatic influences within major communities is further seen in the absence of appreciable variation in the majority of deciduous and coniferous forest species here considered. Space does not permit a full discussion of these and other important factors in variation; we wish only to call attention to the apparent relations of variation to community dynamics and distribution.

The evolution of birds doubtlessly involves the fitting of each species into an ecological niche, that is, a particular position in the biotic environment in relation to shelter, food, and predators.⁴ This niche may be sparse or it may be fairly widespread, and the confinement of a species to it may be determined by one or more of a number of controlling factors including the adaptability of the species, the availability and extent of the niche itself, etc., as well as the much-emphasized climatic factors. A true climax indicator appears to be con-

⁴ The niche of a particular species is obviously difficult to define and entails an extensive study of environmental relations. However, one refers to the niche most conveniently in terms of the place within the environment characteristically frequented by the species. Thus, in the case of birds, this would usually be vegetation type.

fined to a niche which is available only within that climax, and subspecific variation, if present at all, is not as extensive as in most subclimax species. Other than those examples from the deciduous and coniferous forest and grassland given in this paper, Grinnell (1927) has shown the same relation of a species to a climax in the case of the California thrasher (*Toxostoma redivivum*), a species of the coastal chaparral association. This may involve an influence of broad climatic factors controlling the climax, but more likely it also involves the influence of the secondary climate created by the vegetation — the 'microclimate.' However, whether it is one factor or a multiple of factors, the community relation, as Trotter (1912) and Dice (1922) have pointed out, is still present and worthy of the emphasis which it is given here.

The direct control of vegetation as a factor in bird distribution has been shown in local studies by a rather small number of workers (e.g., Kopman, 1907; Adams, 1909; Gates, 1911; Chapin, 1923; Saunders, 1936) and in regional studies only in Trotter's (1912) sketch of North American faunal divisions. Adams (1909) pointed out the importance of a knowledge of the successional relations of vegetation as the controlling elements of and key to the local distribution and relations of birds and emphasized that before progress could be made in an understanding of evolution of birds themselves, extended studies of the interrelations of birds and vegetation would have to be made.

Throughout this paper we have dwelled on niche and community relations but do not intend it to be a contribution to the "present disposition to minimize greatly the effect of temperature" (Murray, 1939) or any other physical factor. Rather, by contrast, it is an attempt to stress the importance of biotic factors — the importance of the ecological niche as it is affected by vegetational control, community relationships, interspecific competition, etc. Among birds, the delimiting effect of physical factors is difficult to ascertain; it is often indirect by dint of the climate-vegetation relationship. Biotic factors, which are equally and possibly the more immediate, have received too little attention. It would seem that the analysis of the effect of physical factors on species distribution must necessarily be preceded or accompanied by an evaluation of the more evident and immediate ecological relationships.

Some life zone adherents point out that since both birds and vegetation are affected by other factors, such as climate, vegetation is not important. While each species may have a characteristic set of physical extremes marking the limits of its tolerance, this does not necessarily overshadow the importance of vegetation control and numerous examples of its effect can be given. The spread of the chestnut-sided warbler (*Dendroica pennsylvanica*) through shrubby second growth in cut-over areas of the northeastern states, the spread of the olive-sided flycatcher into planted conifers in so-called 'Upper Sonoran Zone' in California, the breeding of the blue-headed vireo (*Vireo solitarius*), a species of the coniferous forest climax, in subclimax pines within the 'Upper Austral Zone' of the deciduous forest region, the spread of the prairie chicken into the northwest with the clearing of land — all of these indicate the fidelity of species to some life-form of plant within which or along which the ecological

niche they require is made available but which they will not occupy outside of their normal or original ranges if other physical factors exceed their limits of tolerance. In addition to niche requirements, agreements in distribution with climax communities may represent approximately similar ranges of tolerance to climatic factors.

Frequently, the cyclic nature of climatic factors may strike such a combination of circumstances that if a species, normally a non-breeder within an area, is present and the conditions, both physical and biotic (particularly vegetation), resemble those of its normal breeding range, it may breed as in the case of pine siskins (*Spinus pinus*) in Nebraska (Swenk, 1929) and the olive-sided flycatcher and red-breasted nuthatch (*Sitta canadensis*) on Little Mountain in northeastern Ohio (Bole, in correspondence). This illustrates the effect of physical factors in addition to the direct control of vegetation. More likely, the direct control of physical factors can be better determined in those species which are characteristic of subclimax situations or of some particular life-form, be it climax or subclimax, as in the case of the downy woodpecker. The confinement of a species to particular portions of an area over several biomes in which the niche is available would certainly appear to be an expression of climatic delimitation. However, this might again involve a niche-relationship (i.e., interspecific competition) as in the case of the different species of woodpeckers in the southwest filling up a niche which might be occupied by the downy woodpecker.

During the past thirty years, life zones have provided ornithological literature with pages of discussion. In various distributional studies as those of Robert's 'Birds of Minnesota' (1932) and Eaton's 'Birds of New York' (1906), one finds lengthy explanations of how life zones are 'modified' in those particular states or areas and upon analysis this modification brings bird distribution into direct correlation with vegetational types rather than with life zones based on temperature. The discussion is, therefore, lengthened by the process of going from birds to zones and back to vegetation instead of from birds directly to vegetation. Practically all detailed studies of life zones have been more or less local in nature, and with the exception of Merriam's studies (1890, 1894), they do not cover an area larger than one of the states. In most cases the bounds of such areas are, therefore, political and any agreement within them rarely carries over into other parts of a natural area, the same holding true for species selected as indicators. Thus Howell (1921) calls Bachman's sparrow (*Aimophila aestivalis*) a Lower Austral bird in Alabama, while Brooks in West Virginia (1938) debates its affinities with the Upper Austral, Transition, and even Canadian zones. Another example — Howell's Upper Austral indicators include the robin (*Turdus migratorius*) and ovenbird, both of which range up into the Canadian Zone, the former even into the Hudsonian Zone.

Discussions of life-zone relations frequently overlook the seral relations of birds. Thus, Wright and Allen (1910) discuss the spread of 'Austral' birds — the grasshopper sparrow (*Ammodramus savannarum*), towhee (*Pipile erythrophthalmus*), and chat (*Icteria virens*) — into the Ithaca region of New York, which lies within the deciduous forest-coniferous forest ecotone. Within the deciduous

forest biome, these are seral-stage birds occurring in fields and meadows in the case of the first species, shrubs and forest edge in the case of the second and third, niches which the activities of man more so than any other factor have probably made available in the Ithaca region. Given time, succession to a climax forest would again eliminate these species and confine them to the areas where the organization of plant communities as regards the prevalence of certain life-forms provides them with the ecological niche to which they are limited. An appreciation of the laws of succession can do much towards a clearer understanding of bird distribution and the 'spreads' and 'disappearances' of various species.

The most successful application of life zones occurs where vegetation coincidentally agrees with them and where, therefore, there has been no need to 'modify' zones to make them fit the facts of bird distribution. Thus, the tundra (Arctic Zone), the tundra-coniferous forest ecotone or sub-arctic forest (Hudsonian Zone), and the coniferous forest (Canadian Zone) consist of two distinct plant formations with distinct faunae; therefore, they are distinct biomes, and obviously indicator species would be numerous. While the extensive ecotone between them has species of its own (e.g., gray-cheeked thrush (*Hylocichla minima*), northern shrike (*Lanius borealis*), pine grosbeak (*Pinicola enucleator*), etc.), it is hardly of the same order as the other two 'zones' inasmuch as it is actually a transition zone and certain species of both biomes occur within it. Thus, the willow ptarmigan, a tundra species occupies the tundra-coniferous forest ecotone as well as the olive-sided flycatcher, a coniferous forest species, while the third combination of life forms — conifers more or less stunted and scattered in open tundra — is occupied by the characteristic species mentioned. These zones are transcontinental, they are natural units, and the correlation is good. But they are made of two biomes with a broad ecotone in between, and the application of Arctic, Hudsonian, and Canadian to what is tundra, ecotone, and coniferous forest is unnecessary as well as non-clarifying. However, south of these zones, so-called indicator species do not withstand critical examination as Murray (1939) has admitted. Any zonal agreement in the deciduous forest region is lost westward in the grasslands, for no transverse belts can be recognized in the natural unit which extends from southern Canada to Mexico, and beyond that, the continued application of the same set of terms to several totally different biotic formations and their major and minor divisions is very confusing and incorrect.

Murray's recent paper (1939) illustrates the reluctance of ornithologists to drop the life-zone concept in the absence of an alternative. While he admits the failings of zones and shows an understanding of some of the dynamics of bird distribution which provide him with grounds for deserting the zone concept, he holds that it can be reconstructed though he does not state upon what basis. Assuming this to be the prevailing attitude, the primary need is an explanation of the concepts of modern ecology applied to the facts of bird distribution to illustrate the main points. Much progress could be made if the stumbling block which the pseudo-finality of life zones has placed before avian zoogeographers could be removed.

Summary

1. For the past 50 years, North American ornithologists have adhered to Merriam's life-zone concept in analyzing the facts of bird distribution.

2. The life-zone theory has been examined critically both from the experimental and faunistic aspects, and in no way does it clarify, but rather misrepresents the relations of biotic communities.

3. The concepts of modern ecology as an alternative view are considered briefly through an application of them to twenty-seven species of North American birds to show the relation of their distribution to major biotic communities. North American Tetraonidae as a taxonomic group, eleven species commonly associated with the deciduous forest, and four coniferous-forest species were tested for correlation with biomes by plotting local occurrences on individual maps.

4. The fundamental and largest unit of plant-animal communities is the biome. A diagram and map of the major communities of North America show the relationship and relative size of the climaxes together with broad ecotones and extensive subclimaxes.

5. Designation of breeding ranges of birds are usually inadequate due to a lack of evaluation of abundance and a lack of appreciation for the importance of community relations. In ten species of deciduous-forest birds, breeding ranges are differentiated into areas of common, uncommon, and rare occurrence within the community occupied by the particular species.

6. Three species of Tetraonidae are characteristic of the tundra biome, four of the coniferous forest biome, and three of the grassland biome; two species are characteristic of seral stages rather than of any climax and range over three or four biomes.

7. Seven of the eleven deciduous forest species are confined to that biome; two occupying climax deciduous growth within the biome occur in subclimax vegetation of the same life form in the coniferous forest biome; one species, *Dryobates pubescens*, occurs in deciduous growth over all of temperate North America. A race of the last species (*Antrostomus vociferus*) is confined to the deciduous forest region; other races while occurring in different climatic regions (chiefly Mexico), are found in communities in which the combination of vegetational life-forms appear comparable to the subclimax niche of the deciduous-forest race.

8. Correlation of birds with vegetation reveals no relation to specific dominants or groups of dominants of a single biome; consistent correlation, however, occurs between species and life forms of plants.

9. In species ranging over several biomes variation tends to show correlation with climatic factors; among species confined to one major community variation appears to be effected by geographic and biotic factors.

10. A true avian indicator of climax communities is confined to a niche which is available within that climax and barring biotic and geographic factors, does not vary subspecifically.

11. Distribution of birds confined to a biome may be controlled more by availability of the niche while species characteristic of seral stages in more than one biome may be limited more directly in distribution by physical factors.

12. A clearer understanding of the facts of bird distribution can be obtained through an appreciation of the laws of biotic succession and recognition of developmental as well as climax biotic communities over the continent.

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REFERENCES

- ADAMS, C. C. 1909—An ecological succession of birds. Chap. V, pp. 121-154 in *An ecological survey of Isle Royale, Lake Superior*. Rept. Bd. Biol. Surv. Mich. 1908, 468 pp.
- ALLEN, J. A. 1871—A sketch of the bird faunae of eastern North America. *Bull. Mus. Comp. Zool.* 2:375-425.
- AMERICAN ORNITHOLOGISTS' UNION. 1931—Check-list of North American birds. Lancaster, Pa., 4th ed., 526 pp.
- BATCHELDER, CHARLES FOSTER. 1918—Two undescribed Newfoundland Birds. *Proc. New England Zool. Club* 6:81-82.
- BENT, A. C. 1932—Life histories of North American gallinaceous birds. *U. S. Nat. Mus. Bull.* 162: 477 pp.
- BIRD, RALPH D. 1930—Biotic communities of the aspen parkland of central Canada. *Ecology* 11:356-442.
- BRAND, DONALD D. 1936—Notes to accompany a vegetation map of northwest Mexico. *Univ. New Mexico Bull., Biol. Ser.* 4:1-27.
- BROOKS, M. 1938—Bachman's sparrow in the north-central portion of its range. *Wilson Bulletin* 50:86-109.
- CARPENTER, J. RICHARD. 1939—The biome. *Amer. Midl. Nat.* 21:75-91.
- CHAPIN, J. P. 1923—Ecological aspects of bird distribution in tropical Africa. *Amer. Nat.* 57:106-125.
- CLEMENTS, F. E. AND V. E. SHELFORD. 1939—*Bio-ecology*. New York, 423 pp.
- CONOVER, H. B. 1935—A new race of ruffed grouse from Vancouver Island. *Condor* 37:204-206.
- DAUBENMIRE, R. F. 1938—Merriam's life zones of North America. *Quar. Rev. Biol.* 13:327-332.
- DICE, L. R. 1922—Biotic areas and ecological habitats as units for the statement of animal and plant distribution. *Science* 35:335-339.
- 1923—Life zones and mammalian distribution. *Journ. Mammalogy* 4:39-47.
- EATON, ELON HOWARD. 1910-1914—*Birds of New York*. N. Y. State Mus. Memoir 12, 2 vols.
- GATES, F. C. 1911—Summer bird life in the vicinity of Havana, Illinois, in its relation to the prominent plant associations. *Wilson Bulletin* 23:1-27.
- GRINNELL, J. 1917—The niche-relationships of the California thrasher. *Auk* 34:427-433.

- 1927—The designation of birds' ranges. *Auk* **44**:322-324.
- HALLIDAY, W. E. D. 1937—A forest classification for Canada. Can. Dept. Mines & Resources, Forest Service Bull. **89**.
- HOWELL, A. H. 1921—A biological survey of Alabama. *North Amer. Fauna* **45**.
- KENDEIGH, S. C. 1932—A study of Merriam's temperature laws. *Wilson Bulletin* **44**:129-143.
- KOPMAN, H. H. 1907—Aspects of bird distribution in Louisiana and Mississippi. *Auk* **24**:169-181.
- LIVINGSTON, B. E. AND F. SHREVE. 1921—The distribution of vegetation in the United States, as related to climatic conditions. Carnegie Inst. Wash. Publ. **284**, 590 pp.
- MATTOON, W. R. 1937—Forest regions of the United States (map). U. S. Dept. Agric., Forest Service.
- MERRIAM, C. H. 1890—Results of a biological survey of the San Francisco Mountain region and desert of the Little Colorado, Arizona. *North Amer. Fauna* **3**.
- 1894—Laws of temperature control of the geographic distribution of terrestrial Animals and plants. *Nat. Geog. Mag.* **6**:229-238.
- MULLER, C. H. 1939—Relations of the vegetation and climatic types of Nuevo Leon, Mexico. *Amer. Midl. Nat.* **21**:687-729.
- MURRAY, J. J. 1939—Some characteristics of the Canadian Zone in the southern mountains. *Raven* **10**:1-5.
- NICHOLS, G. E. 1935—The hemlock-white pine-northern hardwood region of eastern North America. *Ecology* **16**:403-422.
- OBERHOLSER, H. C. 1914—Four new birds from Newfoundland. *Proc. Biol. Soc. Wash.* **27**:43-54.
- PETERS, J. L. 1934—Check-list of the birds of the world. Vol. 2. Cambridge, Mass., 401 pp.
- ROBERTS, T. S. 1932—The birds of Minnesota. Univ. Minn. Press, 2 vols.
- RUTHVEN, A. G. 1920—The environmental factors in the distribution of animals. *Geog. Rev.* **10**:241-248.
- SAUNDERS, A. A. 1936—Ecology of the birds of Quaker Run Valley, Allegany State Park, New York. N. Y. State Mus. Handbook **16**.
- SCHMIDT, K. P. 1938—Herpetological evidence for the post-glacial extension of the steppe in North America. *Ecology* **19**:396-407.
- SCHANTZ, H. L. AND R. ZON. Atlas of American agriculture. Part I. The physical basis of agriculture. Section E. Natural vegetation. U. S. Dept. of Agric.
- SHELFORD, V. E. 1932—Life zones, modern ecology and the failure of temperature summing. *Wilson Bulletin* **44**:144-157.
- SHELFORD, V. E. ET. AL. 1926—Naturalists' guide to the Americas. Baltimore, 761 pp.
- SNYDER, L. L. 1939—Great-plains races of sharp-tailed grouse. *Auk* **56**:184-185.
- SWARTH, HARRY S. 1931—Geographic variation in the Richardson grouse. *Proc. Cal. Acad. Sci.* **20**:1-7.
- SWENK, M. H. 1929—The pine siskin in Nebraska: its seasonal abundance and nesting. *Wilson Bulletin* **41**:77-92.
- TROTTER, SPENCER. 1912—The faunal divisions of eastern North America in relation to vegetation. *Jour. Acad. Nat. Sci. Phil.* **15** (2nd ser.):207-218.
- UTTAL, L. J. 1939—Subspecies of the spruce grouse. *Auk* **56**:460-464.
- WEAVER, J. E. AND F. E. CLEMENTS. 1938—Plant ecology. New York, 2nd. ed., 601 pp.
- WRIGHT, A. H. AND A. A. ALLEN. 1910—The increase of Austral birds at Ithaca. *Auk* **27**:63-66.

Observations on *Helodrilus tetraedrus forma typica*¹ and on Other Lumbricidae (Oligochaeta) Found in a Sewage Treatment Plant²

Charles M. Vaughn

For some years members of this laboratory have known of the abundance of certain species of earthworms located in the final settling tank of the sewage treatment plant operated for the twin cities of Champaign and Urbana, Illinois. The writer became interested in making a seasonal survey of these larger Oligochaeta. This study has been carried on in the Zoological Laboratory of the University of Illinois under the supervision of Professor H. J. Van Cleave, whose ready counsel and advice are gratefully acknowledged by the author.

From observations by employees of the sewage treatment plant certain facts concerning the earthworm fauna were evident. During the day in the summer months, the earthworms appear in great abundance on the surface of the rock bed of the trickling filter. With the approach of fall and lower temperatures, they burrow into the rock bed. Under the ten foot layer of crushed stone, the liquid effluent is drained off and piped to the final settling tank. At times many of the annelid worms are washed out in the effluent and pass into the final settling tank. This action has been observed on several occasions by Dr. Max Suter, Engineer of the State Water Survey Division, in his work at this plant on water treatment. Thus samples of the worms living in the inaccessible parts of the filter are washed out into this tank where they continue their existence in an aquatic habitat. The inaccessibility of the lower levels of the rock filter beds for sampling purposes made it impossible to determine if the worms in the effluent and settling tank were an exact, representative sample of those living in the filter. There was a possibility that physical conditions in the filter or physiological states in the worms might have the effect of selecting worms of certain size, age, or physiological condition for elimination from the rock filter beds. As the study progressed, there was an increasing confidence in the assumption that the samples in the effluent from the filter were fair samples of the population in the rock filter beds.

Three species of typically soil inhabiting earthworms were found in relatively large numbers in this study, namely: *Helodrilus tetraedrus*, *Helodrilus sub-*

¹ In the present study, *forma typica* was the only form of *Helodrilus tetraedrus* encountered. All subsequent reference to this form in the present article will be under the abbreviated name of *Helodrilus tetraedrus*.

² Contributions from the Zoological Laboratory of the University of Illinois, No. 559.

rubicundus, and *Helodrilus foetidus*.³ The adaptation of these forms to a strictly aquatic habitat requires distinct changes in feeding habits and possibly changes in seasonal periodicity and growth habits. In the aquatic habitat, both extremes of temperature encountered in the soil by these lumbricids are greatly reduced.

In addition to the Lumbricidae encountered in this survey, a distinct seasonal appearance of large quantities of smaller Oligochaeta of the family Enchytraeidae occurred beginning the latter part of February.

It is the purpose of this study to investigate the seasonal life history of *Helodrilus tetraedrus* as the most abundant species present. Attention was also given to the relative abundance of the other species found in this aquatic habitat.

TABLE 1.—Distribution of Collections Taken from the Final Settling Tank of the Sewage Treatment Plant of Urbana-Champaign, Illinois.

Date of Collection	Number of Worms			Number of <i>Helodrilus tetraedrus</i> forma typica		Number of <i>Helodrilus subrubicundus</i>		Number of <i>Helodrilus foetidus</i>	
	Total	Mature	Immature	Mature	Immature	Mature	Immature	Mature	Immature
10/4/38	147	22	125	15	115	3	7	7
10/18/38	134	17	117	17	115	2
11/1/38	558	129	429	127	421	2	8
11/19/38	612	319	293	316	289	2	1	1	3
11/29/38	619	475	144	470	144	5
12/27/38	665	517	148	437	135	80	6	7
1/12/39	724	648	76	400	74	213	2	35
2/18/39	591	488	103	307	94	147	2	34	7
3/18/39	(See Below for Data on this Collection)								
4/8/39	(See Below for Data on this Collection)								
4/29/39	776	669	107	621	100	36	12	7
5/20/39	632	494	138	485	133	9	4	1
6/9/39	592	463	129	380	33	10	18	73	78
9/30/39	896	225	671	214	640	1	6	10	25
10/23/39	948	748	200	747	200	1
11/6/39	1,247	798	449	798	448	1
11/20/39	1,067	724	343	712	340	12	2	1
Totals	10,208	6,736	3,472	6,046	3,281	516	45	174	146

MATERIALS AND METHODS

Collection and Fixation.—Periodic collections of material were taken from the central portion of the western wall of the final settling tank. In the laboratory, anaesthetization and fixation were carried on under as nearly standardized conditions as possible to avoid sources of error in comparing the various collec-

³ In the literature on the Lumbricidae, there is wide variation in the nomenclature followed by different authors. For the present report, the names accepted by American authorities have been used except that subgeneric names have been omitted to avoid confusion. Many workers have subdivided the genus *Helodrilus* so that the following names are in use: *Helodrilus tetraedrus* forma typica = *Eisenia la tetraedra* forma typica; *Helodrilus foetidus* = *Eisenia foetida*; *Helodrilus subrubicundus* = *Dendrobaena subrubicunda*.

tions. About 20 worms were placed in a large, covered, glass crystallizing dish containing sufficient dechlorinated water to cover the bottom of the dish. A small amount of chloroform in a Syracuse watch glass was lowered into the water in the dish.

In general, the process of fixation follows that suggested by Welch (1913) with a few modifications. As a fixative, a mixture of 1 part of 40% formaldehyde and 9 parts of 85% ethyl alcohol was used. The annelids were dipped into the fixative and were immediately removed and extended upon paper towelling. After a few moments, the straightened worms were immersed in the fixative for 2 or 3 hours to harden. The material was then transferred to 85% alcohol and kept for later study.

Table 1 serves as a summary of the general scope of the survey, showing the date and total number of individuals included in each collection. The additional columns indicate the relative numbers of each species of mature and immature Lumbricidae found in the samples.

In Table 1, the records for the March 18, 1939, and April 8, 1939, collections are blank because of a great reduction in the lumbricid fauna. The limited number of large annelids found on these dates were utilized in laboratory experiments on effects of overcrowding. In the present study, attention was at first directed to the larger oligochaetes (Lumbricidae) only. However, on February 18, 1939, the sample contained numerous Enchytraeidae which continued as the most important annelids during the months of March and April. Then they disappeared entirely or became very uncommon throughout the remainder of the year. Due to their fragility and small size, a different method of fixation was essential. If a limited number of these forms were placed in a Petri dish, they would remain on the bottom, often in a tangled, interwoven mass. A small watch glass containing chloroform was placed in the water and in a short time the worms were completely anaesthetized. It was found that at this point the annelids could be transferred directly into 85% alcohol and preserved for further study.

Experiments.—The density of population of earthworms in the final settling tank is very much greater than is ever encountered among the same species of oligochaetes living in soil. A series of experiments was designed to attempt to establish the tolerance to overcrowding of the various species concerned in this study. The annelids used in these experiments were the large lumbricids collected on March 18, 1939. Twenty-five specimens of *Helodrilus tetraedrus* were placed in a large glass dish containing dechlorinated water to a depth of $1\frac{1}{2}$ inch. A second dish contained 100 individuals of this species in an equal volume of water. A set of dishes was also set up, one containing 25, the second 50 *Helodrilus foetidus*. Similarly, a single dish containing 20 *Helodrilus subrubicundus* completed the series. The water in each dish was changed daily.

The study of lumbricids maintained in the laboratory demonstrated a few isolated facts pertaining to the habitat under consideration. The specimens of *Helodrilus subrubicundus* remained alive for 6 days submerged in water. Specimens of *Helodrilus foetidus* remained alive 3 days longer in the dish containing fewer individuals. These forms were all dead after 11 days. The

first fatality in a dish with only 25 *Helodrilus tetraedrus* occurred on the 15th day, 10 days after the first recorded deaths in the dish containing 100 individuals. The entire series was destroyed on the 23rd day as a result of a sudden increase in the laboratory temperature during the preceding 24 hours.

Observations.—The study of the preserved Lumbricidae began with the separation of the mature worms which bore the prominent spermiducal pores and the clitellum, at least its beginning ridges. While the diagrammatic key of Olson (1928) was satisfactory for identification of the mature worms, color patterns were found available for separating the immature individuals and associating them with the mature worms of the respective species. From this process of separation and classification, Table 1 shows that there were only three distinct species of Lumbricidae present in all the samples taken from the final settling tank. They were, namely: *Helodrilus tetraedrus* forma *typica*, *Helodrilus subrubicundus*, and *Helodrilus foetidus*.

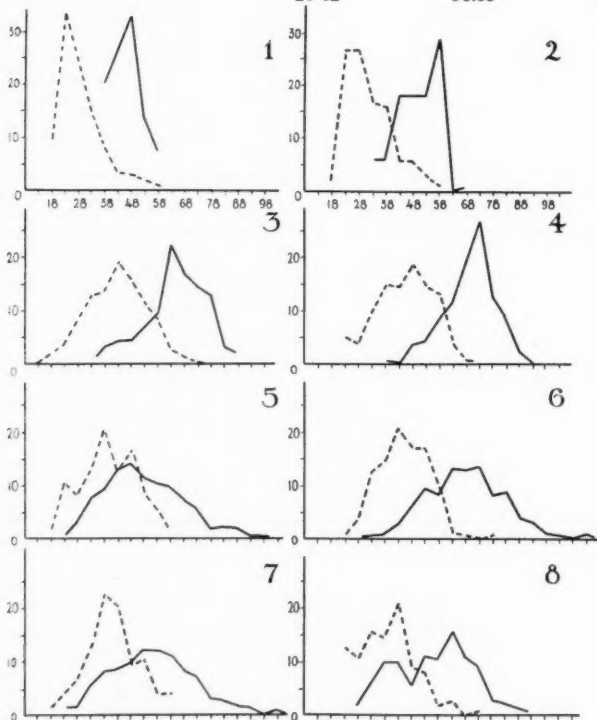
Again referring to Table 1, *Helodrilus tetraedrus* is the only species which appeared in all the samples taken. Because of the constancy of this species' appearance, it was selected for the purpose of studying the seasonal growth rate and the reproductive habits by means of a statistical analysis of the measurements of the lengths. As the study progressed consistent results showed markedly greater lengths for these mature worms than the literature recorded. From subsequent collections, specimens were placed individually in large glass dishes allowing them to extend, contract, and move about freely. The length could be estimated with a fair degree of accuracy by holding a millimeter rule above the animals as the fully extended animals tended to remain quiescent for several minutes. Comparing these individual measurements with those of the same specimen after fixation, the two measurements agreed with a maximum variation of two or three millimeters in each case. As the lengths of the individuals usually were 10 or more mm. longer than the recorded lengths in the literature, this check of the method of fixation demonstrated that the fixation was not responsible for the extreme length of the worms encountered in the present study.

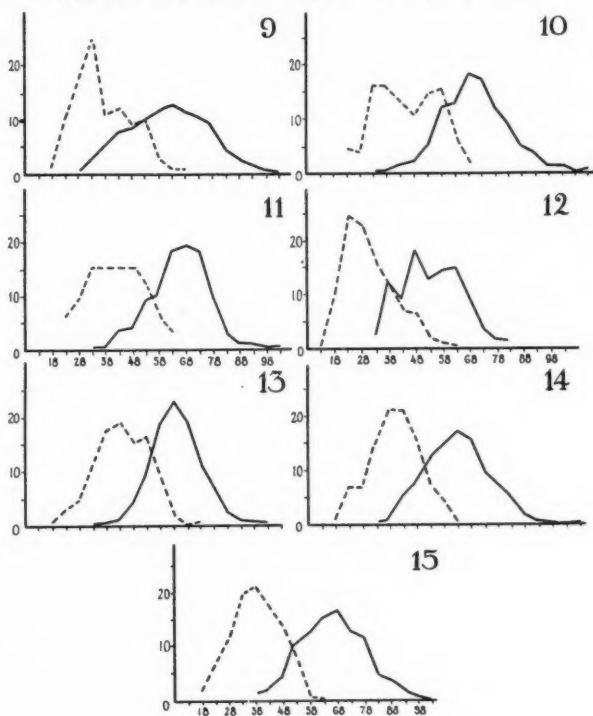
EXPLANATION OF GRAPHS

The graphs show the distribution of mature (solid lines) and immature (broken lines) *Helodrilus tetraedrus* forma *typica* for each collection. The ordinate represents the percentage of each collection found in 5 mm. size groups tabulated along the abscissa. In the following table for each collection the first set of values is for mature individuals and the second for the immature individuals.

Graph Number	Collection Date	Range in mm.	Mean in mm.	Mode (crude) in mm.
1	10/4/38	36-58 17-56	45.67 28.61	48 23
2	10/18/38	34-70 20-57	50.65 31.74	58 25
3	11/1/38	34-87 14-71	64.30 42.73	63 43
4	11/19/38	38-96 22-95	69.39 45.15	73 48
5	11/29/38	21-102 20-62	53.37 39.63	48 38
6	12/27/38	25-118	67.92	73

7	1/12/39	25-76	45.15	43
		23-110	56.65	55
8	2/18/39	20-63	40.91	38
		30-100	56.03	63
	3/18/39	21-73	39.12	43
	4/8/39	-----	-----	-----
9	4/29/39	30-106	61.78	63
		20-68	37.50	33
10	5/20/39	32-111	71.47	68
		21-68	44.96	35
11	6/9/39	35-103	65.58	68
		24-67	42.39	40
12	9/30/39	32-83	54.15	48
		15-61	30.78	23
13	10/23/39	34-100	64.12	63
		20-72	43.83	43
14	11/6/39	35-106	62.91	63
		20-72	39.99	38
15	11/20/39	37-105	66.77	68
		20-62	38.68	38





RESULTS

In attempting to determine the seasonal life history of *Helodrilus tetraedrus*, statistical methods have been employed in the hope that the mode, the mean length, the range, and the percentages of the total collections in the different class intervals might reveal seasonal growth trends in a seasonal progression within the limits of this survey. In the Explanations accompanying the Graphs, the summary of the tabulated data is shown, giving the range of the length of the animals examined in each collection, the mean length, and the mode for each collection. The mean length was determined by means of

the statistical formula $M = \frac{\sum fd'}{n}$ (—). In this formula: M is the mean,

AM is the assumed mean, (i) is the class interval which is the range between the midpoint of two successive groups and in this study remains constant with

a value of 5 mm. for all of the collections, (—) stands for the sum of (\sum)

the frequencies (f) multiplied by the deviation (d') from the assumed mean and this result is then divided by the total number of individuals (n) present in the sample. The modes in the Explanations accompanying the Graphs represents the class value of the interval or group containing the largest number of individuals in a given sample.

In Graphs 1-15 showing the ranges of the individual collections, it is evident that there is no definite length reached by this lumbricid prior to its reaching maturity. In this regard, *Helodrilus tetraedrus* differs conspicuously from forms which have been studied previously in this laboratory. In all of the Mollusca and Crustacea which have been studied, there has been distinct correlation between size and age especially as reflecting the degree of sexual maturity. It seems evident that increased size in *Helodrilus tetraedrus* does not assume the physiological importance that it does in the Mollusca and Crustacea where shell and exoskeleton offer distinct limits to expression of body size and sexual maturity. All collections show many immature worms of a size equal to or greater than many of the mature individuals.

Immature worms were found in the final settling tank at all seasons of the year. However, there was no season when very small worms appeared in such numbers as to give evidence that the worms were breeding in the final settling tank. The exact time and place of reproduction in this habitat have not been determined. The collection of June 9, 1939, (Graph 11) contained the smallest representations of small, immature worms of all the collections taken throughout the year. The occurrence of greatest number of smallest individuals in the September 30, 1939, (Graph 12) collection gives evidence of greatly increased reproductive activity since the time of the June collection.

By further analysis of the September 30, 1939, collection, approximately 40% of the immature individuals are found in the 31 to 55 mm. range. These are included in the range of the mature worms of this and the succeeding collections. At the time of the next collection, the immature worms show a decrease in their relative number compared with the mature worms found in this collection. However, 79% of the immature worms of the October 23, 1939, collection (Graph 13) are found in the 31 to 55 mm. range. In the November 19, 1938, collection (Graph 4), 86% of the immature forms were located in the 31 to 60 mm. range. In the November 20, 1939, collection (Graph 15), 88% of the immature worms were in the 26 to 55 mm. range.

The September collection has 12% of the sample of mature worms included within the range of 36 to 40 mm. These worms range very close in size to a large portion of the immature worms included in this sample. Their abundance seems to furnish evidence that between the June and September collections, the reproductive activity in this form has been greatly accelerated over what it had been in any other similar period during this study. Reproductive activity had been continuing on a smaller scale throughout the survey as evidenced by the fact that immature specimens were present in all samples taken during the survey.

In the next collection, (Oct. 23) 50% of the mature worms are within the

limits of 51 to 65 mm. For the most part these individuals have reached maturity since the preceding collection. There is no large group of mature worms until the 50 mm. size is reached. The mature forms present in the September collection in the 36 to 40 mm. group must have increased in size to fit into this new grouping found in the October collection. The mean size of the immature forms has increased about 13 mm. between Sept. 30, and Oct. 23, 1939. This increment in length if equalled in the mature forms would easily account for the increased size from the 36 to 40 mm. group to the 50 to 55 mm. group bringing this group within the limits of the major portion of the mature worms.

The collection of November 6, 1938, has a similar range of mature forms, being 51 to 70 mm. for 60% of the sample. There seems to be little change in the size of the immature forms if the mean is observed. However, 60% of the immature worms in the October collection were found to be between 41 and 60 mm. This group is very close to the limits for the major portion of the mature worms in the next collection. Here again the immature forms seem to increase their morphological differentiation resulting in the development of the external sexual features used to differentiate the mature from the immature worms.

In the November 20, 1939, collection, a range of 51 to 70 mm. will include 55% of the mature worms of the sample. The means for the immature worms for this and the preceding collection vary by less than two millimeters. The earlier November collection included 48% of the immature worms within a range of 41 to 60 mm. Here again the immature worms of one collection appear to have matured and the remaining portion have increased sufficiently in size to again present a similar ratio in the final collection as evidenced by the closely related mean average lengths of the two collections.

This continuity of the mean throughout these collections points to a constancy farther back in the study. To maintain this constancy of length it was necessary to have had a continued production of worms during the period between June and September. If such were the case the worms which began development earlier would reach maturity earlier and if there is a constant change in the collections from immature stages in one collection to mature forms in the next there must necessarily have been a constant productivity of worms over a two to three month period.

The data have shown that following this period of accelerated reproductive activity between June and September, there is a period of growth and maturation continuing from September to November in which the majority of the mature individuals are found within a range of 50 to 70 mm. Forms which are of greater lengths must then represent individuals which began development prior to this period of high reproductive activity or have better adapted themselves to this habitat.

There is little that can be said about the other species encountered in this study. In Table 1, the data show scattered representatives of the other species of the Lumbricidae in the survey. There is insufficient material to attach any significance to the large number of *Helodrilus subrubicundus* found in the

December, 1938, January 12, and February 18, 1939, collections or to the increased number of *Helodrilus foetidus* present in the June collection.

In reviewing the literature in which descriptions of *Helodrilus tetraedrus* appear, the authors uniformly cite the length of mature individuals as being between 4 and 6 cm. Study of Graphs 1-15 shows large numbers of individuals are found above this limit as follows:

November 19, 1938	70%	June 9, 1939	70%
December 27, 1938	60%	October 23, 1939	63%
February 18, 1939	41%	November 6, 1939	55%
April 29, 1939	50%	November 20, 1939	65%
May 20, 1939	74%		

Also in a few collections there are instances where the lower limit of 4 cm. for mature worms excludes a sizable part of the sample as follows:

November 29, 1938	20%	February 18, 1939	17%
January 12, 1939	17%	September 30, 1939	12%

The range which has been given for the length of mature individuals appears to be somewhat small in view of the data tabulated here. This increased size may be a response to an aquatic habitat rich in organic matter but lacking the physical obstacles present in the soil.

Overcrowding, as studied in the laboratory, seemed to play an important role in the habitat relations of these forms. This view was further substantiated at the time of the next field collection. On April 18, 1939, the extremely abundant earthworm fauna was again almost exclusively of the Enchytraeidae, and large masses of dead Lumbricidae were found in the settling tank from a depth of 8 to 18 inches below the surface of the water.

The much greater resistance of *Helodrilus tetraedrus* shows it can adapt to this habitat more readily than the other species. This may in part account for the greater abundance of this species in this habitat.

In the laboratory studies, a steady inflow of constantly moving water was not available in the dishes in which the worms were kept. Activity in the settling tank furnishes a considerable degree of aeration along the western wall of the settling tank. The oxygen content of the water is probably a limiting factor to the distribution of the lumbricids in the tank. In all collections, the author found the worms along the wall within 6 to 8 inches of the water's surface. Below this region only the dead bodies of annelids were ever found.

The most abundant member of the earthworm fauna during March and April, 1939, was a member of the family Enchytraeidae, which first appeared in the samples in the latter part of February. These forms were not encountered in any of the other samples taken during the period of this survey. Due to their seasonal appearance they were considered incidental to the life history study in progress and no further observations of these forms are included here.

SUMMARY

This study consists of 17 collections taken during the period from October 4, 1938, to November 20, 1939, from the western wall of the final settling

tank of the Sewage Treatment Plant operated for Champaign and Urbana, Illinois.

The total number of lumbricid worms studied was 10,208 of which 6,736 were mature lumbricids and 3,472 were immature individuals. There were included 6,046 mature specimens and 3,281 immature specimens of *Helodrilus tetraedrus* forma typica; 516 mature and 45 immature specimens of *Helodrilus subrubicundus*; 174 mature and 146 immature specimens of *Helodrilus foetidus*.

As *Helodrilus tetraedrus* composed about 90% of the entire sample and was the dominant species present throughout the main part of the study, it was selected for the seasonal study of its life history.

From the small amount of data concerning *Helodrilus foetidus* and *Helodrilus subrubicundus*, it appears that these forms are relatively scarce in this habitat.

The difference in the mean length of the immature worms between the September and October collections of 13.06 mm. appears to be the average monthly size increment of the collections made. The continuity of the mean length of the immature forms in the succeeding collections shows a constancy existing for a period of approximately three months' duration. This was preceded by a period of reproductive activity of a similar length occurring between the time of the June and September collection (Graphs 11 and 12).

The succeeding period from September to November appears to be the period of growth and maturation of the forms which developed during the period of high reproductive activity in which they reached a length of 50 to 70 mm. Forms with lengths greater than this range may be individuals which began development before this period of accelerated reproductive activity or individuals which have better adapted themselves to the habitat.

The presence of immature forms throughout the survey shows that reproductive activity occurs throughout the year but at an accelerated rate during the summer months.

The increase noted in maximum length of mature individuals gives evidence of better growth conditions existing in this habitat over those found in the normal soil habitat.

Overcrowding exerts a marked influence upon these worms both in the laboratory and in the settling tank. It appears that the oxygen content of the water may be a limiting factor upon the vertical distribution of the lumbricid fauna restricting their sphere of activity to a depth of 6 to 8 inches at the water surface of the final settling tank.

The distinct, seasonal appearance of a member of the family Enchytraeidae was noted during the months of March and April in this study.

REFERENCES

- OLSON, HENRY W. 1928—The Earthworms of Ohio. Ohio Biological Survey, Bull. 17, 4(2):47-90.
WELCH, P. S. 1913—A Method for the Preparation of Earthworms and smaller Oligochaetes for Study. School Sciences and Mathematics 13:15-18.

Relationships within the Family Chrysomelidae (Coleoptera) as Indicated by the Male Genitalia of Certain Species¹

Eugene F. Powell

Introduction

The last quarter century has seen the use of the genital characters of insects come into prominence as a means of accurate identification of species. The increased use of such characters has been due, in part, to the ineffectiveness of color and other superficial differences which are affected by environment, such characters having been used in many early contributions to the taxonomic literature. The adult genitalia, which in many groups lie wholly within the insect body, except during copulation and oviposition, are less liable to be affected by environmental factors and, therefore, should supply more reliable characters for species distinction. In addition to the internal position of these structures, especially in the Chrysomelidae, they are usually heavily chitinized and would not be easily modified.

A study of these structures as they are found in the males of certain species of the Chrysomelidae has been made by the author. The distinctions between different species have not held his interest so much as the broader investigation of the relationships which must exist within the group. If species differences in the genitalia are found to be definite it seems logical to suppose that from them phylogenetic relations could also be determined with some degree of accuracy. It has been with this latter aim in view that the present study has been made.

A review of the literature on the subject reveals that many workers with insect genitalia have shown that these genitalia are derived from originally paired structures. Notable among the contributions which support this fact are those of the following: Christophers and Cragg (1921-1922) in Hemiptera (*Cimex*), Singh-Pruthi (1925) and George (1928) in Homoptera, Christophers (1922) in Diptera (*Mosquito*), Haviland (1921), Kraepelin (1873), Kulagin (1897-1898) and Michaelis (1900) in Hymenoptera, Zander (1900, 1901, 1903) in Hymenoptera, Trichoptera, and Lepidoptera, Verson and Bisson (1896) in Lepidoptera, and Newell (1918) in insects in general; Singh-Pruthi (1924) and Metcalfe (1932) have studied the development of the genitalia in Coleoptera and agree as to the exact structures from which the genitalia are derived. Muir (1918) who has also studied the development of the genitalia states that the "median lobe" (intromittent organ, penis, aedeagus) develops as an unpaired median element.

If the findings concerning the double origin are true, it would seem that the adult genitalia which show the most indications of such origin should first

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be determined and from this tentative ideas of phylogenetic relationships made. This would necessitate that the adult genitalia be well investigated and then checked with their embryological development. The former has been the plan of the present study. It is hoped that future investigations upon the development of some genitalia discussed herein may be made.

Originally the plan of this investigation included the study of male genitalia from one species of each genus within the family Chrysomelidae as found in North America. The difficulties involved in obtaining representatives of all genera, — due to restricted distribution, scarcity and the impossibility of exchanging and collecting certain species needed, — accounts for the limitation to those species which could be procured. Several species of certain genera have been included to give indications of relationships which must exist within these smaller groups. Although the results concerning relations existing between the genera cannot be as conclusive as was desired it is hoped that this study may contribute toward a better understanding of this large family of beetles.

The nomenclature of the species is that of Leng's "Catalogue of the Coleoptera of America, North of Mexico" (1920) with a few recent changes indicated by Barber and Bridwell (1940). All of these changes are plainly indicated in the section on the Descriptions of the Genitalia. The descriptions and drawings are arranged in the order given in the above mentioned publication.

The writer wishes to acknowledge his indebtedness to the late Dr. Robert H. Wolcott of the University of Nebraska under whom this study was first begun; to Dr. David D. Whitney for helpful suggestions during the preparation of the manuscript; to Dr. H. W. Manter for suggestions concerning drawings and for aid with the photographic work entailed; to Dr. George Hudson who generously donated specimens for study; and to the Department of Zoology of the University of Nebraska for the provision of facilities for the progress of the work and also for the purchase of certain specimens which were not otherwise available. Helpful suggestions were also made by Professors Myron H. Swenk, Don B. Whelan, and Raymond Roberts of the Department of Entomology of the University of Nebraska. The names of several specimens were verified or corrected by Mr. H. S. Barber of the Division of Insect Taxonomy of the United States National Museum. Such species are indicated (B) in the manuscript and acknowledgment of indebtedness to this source of reliable information is here made. Due credit is also given to Dorothy M. Powell who, in addition to the care of six children, found time to aid with the reading of the manuscript and to offer encouragement so necessary for the completion of such work.

Materials and Methods

The specimens used in this study were obtained from various sources throughout the United States and Canada. A considerable number were Nebraska specimens collected by the author during the last ten years. Others taken in various parts of the United States were donated by friends or were obtained by exchange or purchase. Of the one hundred seventeen genera listed by Leng (1920), representatives of fifty-one genera including seventy-two species were studied. All subfamilies were included except four, namely, Sagrinae, Megascelinae, Lamprosominae, and Halticinae. The first three of these groups are small ones containing a total of seven species whose distribu-

tion is limited to southwestern United States. The fourth, Halticinae, is a large subfamily with many species of wide distribution but also many of such small size that the time involved in the dissection of the genitalia made it impossible to include them. Pinned specimens were used for the most part since they were more convenient to handle. Unpinned material was relaxed and pinned. Fresh specimens of local species were also studied.

A serial number was given to each specimen (consecutive numbers to those of a species) and placed on pins and vials used. A progressive record with serial number, collection data, and of the following treatment was kept for each specimen. Additional notes were recorded as a check against mistakes. Various methods of procedure were studied and tried; a combination of those used by Metcalf (1921) and DeLong (1931), with some alterations to meet the needs of the author, was found most suitable.

Relaxation of specimens was accomplished in boiling *distilled* water. The time needed for the different species varied with the chitination but twenty-five to thirty minutes were required to soften the exoskeleton of the heavier insects. No appreciable injury to the colors was noted by this method.

Dissection was done under a binocular dissecting microscope with the aid of various types of curved needles made by the author. In most cases the complete abdomen, or a part thereof, was severed from the body. The remainder was carefully saved on its pin with collection data and serial number. The place formerly occupied by the abdomen was filled with clear shellac to add support to the specimen and was kept for future reference. Such mutilation of the specimens seemed justified since the external abdominal characters were usually not important ones and the extraction of some of the genital parts could be accomplished in no other manner.

During the remainder of the procedure the parts from different specimens were kept separate in one dram vials which were plainly marked with serial numbers of each. The time allowed for the baths in the different solutions was varied slightly according to the chitination of the material, less time being required for that with less chitin.

The abdomens were placed in sodium hydroxide, 10 to 15% strength, and allowed to remain for twenty-four to thirty-six hours until almost clear. Upon removal they were thoroughly washed in distilled water. They were then placed in glacial acetic acid for a few hours to remove any fat and to neutralize any sodium hydroxide which remained after the washing. They were then thoroughly washed in distilled water as before.

The staining required from eight to twenty-four hours (depending on the chitination) in acid fuchsin of the following formula (Metcalf, 1921): acid fuchsin, 1 gram; hydrochloric acid, 10% strength, 25 cc.; distilled water, 500 cc. Specimens usually were heavily stained since a gradual destaining occurred in further handling; a final light stain, best for differentiation for study of parts, was thus obtained.

Upon removal from the stain, the parts were washed and the genitalia were dissected from the abdomens. Delaying the final dissection of the genital

parts until this time reduced the loss of the minute structures desired. A thorough washing in distilled water followed after which the genitalia were stored in one-half dram vials containing glycerin. Each vial was marked with a gummed label on which was printed in waterproof ink the serial number of the specimen, Leng's checklist number, and the name of the species. A coating of collodion was painted over the label as an extra precaution against loss.

Containers for storing the vials, patterned after Schmidt insect boxes, were made from wooden cigar boxes and masonite (synthetic wood). The latter was placed in the bottom of the container and holes of appropriate size and equally spaced were made in it to allow for the insertion of the vials. Lined on the inside with white paper and covered on the outside with heavy black paper these made convenient and permanent receptacles for storage.

A binocular dissecting microscope, a compound microscope, and a deep-well slide were utilized in the study of the genitalia. The specimens were placed in the pit of the slide and submerged in glycerin. This method, since the structures could be turned at any angle, was found much more convenient than permanently mounting them in balsam or damar. When drawings were to be made the specimens were quickly washed in distilled water and fastened in the desired position to the bottom of the well by means of fine lines or smears of LePage's glue before the glycerin was added. When dorsal or dorso-caudal views of curved specimens were needed a small platform was constructed in the well from small pieces of glass slide and the specimens attached to its edge. At first, some difficulties with this method were encountered but with practice they were easily overcome.

Simple line drawings were made with the use of a camera lucida. Such drawings appeared to be easier to understand than many of the complex drawings found in much of the literature which was reviewed. The views chosen seemed to illustrate sufficiently the points desired.

Homology and Terminology

The great variation in the character of the genitalia in the different orders of insects has, no doubt, been responsible for the confusion of terms which have been used for these structures as a group and also for the individual parts. Attempts by many authors to homologize them have somewhat alleviated this situation but much work along this line still remains to be done. The author makes no attempt to give a detailed discussion on this subject but would refer those interested to the contribution of Metcalfe (1932) in which considerable literature is reviewed and a clear discussion of the homologies is given. Since the above mentioned investigation involved the development of genitalia in Coleoptera and included that of *Gastrophysa* (= *Gastroidea* auth.) *polygoni* L., one of the Chrysomelid beetles, the terminology suggested by that author has, in the main, been adopted for the structures considered in this paper.

Investigations into the development of Coleoptera have shown that the posterior segments of the abdomen of the larvae are retracted into the body

and parts and appendages of this retracted portion have been variously modified to form the genitalia of the adult. The name, *genital pocket*, has been used by Singh-Pruthi and Metcalfe for this invaginated portion of the body wall. The other parts of the genitalia are in close relationship to the above structure and, in this paper, have been named the *aedeagus* (Metcalf, Blake, 1932), the *tegmen* (Sharp and Muir, Metcalfe), and the *spiculum gastrale* (Sharp and Muir, also Singh-Pruthi, and Metcalfe).

The first of these has also been called the median lobe by Muir and Singh-Pruthi. It lies within the genital pocket and consists of a median tubular piece, variously shaped and curved in the Chrysomelidae. A portion of the genital pocket near the middle of the aedeagus is chitinized and forms the *tegmen* which partially or wholly surrounds the aedeagus. In most specimens studied by the writer, this structure has the form of a Y with its lateral forks extending from below around the aedeagus while the remainder, the *strut*, projects anteriorly below the aedeagus. In *Macroplea* (= *Haemonia* auth.) *nigricornis* (Kby.), *Donacia piscatrix* Lac., *Orsodacne atra* var. *childreni* Kby. (Pl. 1, Figs. 1, 2, and 3 respectively), and *Timarcha intricata* Hald. (Pl. 6, Fig. 28) the tegmen is united above and forms a *tegmental cap* over the apical (posterior) portion of the aedeagus. Sharp and Muir (1912) have found this condition in many Coleoptera. In the posterior ventral portion of the genital pocket is the *spiculum gastrale*, a Y-, V-, or U-shaped chitinous structure which varies in size and shape. A generalized explanation of the aedeagus and its internal structure, since the latter is not fully represented in the drawings, will clarify the descriptions which follow in a later section.

At its apical end the aedeagus possesses an opening which is here called the *apical orifice* (median aperture of Sharp and Muir). This is usually situated dorso-caudally due to the fact that, in general, its ventral wall forms a more or less, single or double, pointed apex. The median dorsal wall of the aedeagus is usually thinly chitinized in the posterior half. A *basal foramen* (median foramen of Sharp and Muir), which varies in size, is found on the ventral side of the anterior portion. The roof above this latter opening varies in the amount of chitinization and also in extent. In *Orsodacne* and *Timarcha* two elongated plates are separated by a median opening which extends from near the middle to the extreme anterior or basal tip of the aedeagus. Sharp and Muir have also shown that species of these two genera, other than those studied by the author, show this particular character. The same feature, but not developed to such a marked degree, has been noted in other genitalia discussed in this paper.

An *internal sac* (Sharp and Muir) lies within the aedeagus and posteriorly is continuous with it at its apical orifice. The walls of this sac may be membranous (very lightly chitinized) or, as in many cases, provided with chitinized plates. A distinctly chitinous projection from the junction of the internal sac and the dorsal wall of the aedeagus may extend posteriorly above the apical orifice. This structure, which the author has called the *apical hood*, apparently cannot be retracted into the aedeagus. In other species there may be retractile dorsal plates, dorso-lateral plates or no chitinous structures at this point. The

internal sac extends anteriorly within the aedeagus, the distance varying in different species. An *ejaculatory duct* pierces the sac at its closed anterior end and may extend posteriorly within it. In many species, particularly noticed in the subfamily Chrysomelinae (Figs. 28-58 incl.), the ejaculatory duct connects with or passes through a heavily chitinized and larger tube-like structure, the *flagellum* (Sharp and Muir). At or near the closed end of the sac in other species may be found a pair of elongated plates which, because of their position and structure, have been called *ejaculatory guides* by the writer.

The variations of the internal sac and the flagellum, while indicating species differences, have not been studied sufficiently to judge their full significance as to phylogenetic relationships. For this reason the general character of the aedeagus, the tegmen, and the spiculum gastrale are used mainly in further discussion and are fully illustrated and described.

Descriptions of the Genitalia

Macrolepta (= *Haemonia* auth.) *nigricornis* (Kirby) (Pl. 1, Figs. 1a, b, c)

Aedeagus with considerable curve; apex elongated and pointed; apical orifice rather large. Basal foramen large, occupying about one-third of the ventral surface; its borders with thinly chitinized edges which at the anterior tends to curve upward forming a slight pocket. Tegmen ring-like; the strut large and keel-like which when viewed from the side has the shape of the foot of a sock; the lateral, slender and rod-like forks extend dorso-laterally and posteriorly above the aedeagus and join to form a single lobed tegmental cap above the apical orifice; under surface of the tegmental cap curved upward at the tip and bearing long bristle-like hairs. A dorsal plate with two tapering chitinized extensions which curve basally and laterally into the aedeagus is present in the sac at the orifice.

Donacia piscatrix Lacordaire (B) (Pl. 1, Figs. 2a, b)

Aedeagus large, tubular and curved with an elongated and tapering apex. Apical orifice large, occupying about two-fifths of the upper surface. Basal foramen about equal in length to the apical orifice; its posterior edge rather well chitinized and projecting ventrally; the remainder of its border thinly chitinized with anterior edge slightly cupped. Tegmen ring-like, possessing a sock-shaped keel; tegmental cap broad and flattened, divided by a median slit anterior to the tip; the latter bearing long hairs. The internal sac with a median apical hood at the orifice.

Orsodacne atra var. *childreni* Kirby (Pl. 1, Figs. 3a, b, c)

Aedeagus dorsoventrally flattened and only slightly curved. Apex with two pointed lobes. Apical orifice about one-fourth the length of the aedeagus. Basal foramen occupies about one-fourth of the ventral surface, its roof separated by a median slit into two elongated lateral plates. Tegmen ring-like with the strut in the form of a small keel; lateral forks rounded and rod-like and connected dorsally by a transverse rounded ridge; tegmental cap posterior to the ridge having an apex of two pointed lobes, the tips of which are covered with long

hairs. The spiculum gastrale large and Y-shaped, composed of rounded chitinized rods which curl anteriorly upward at their junction. Internal sac large and generally membranous, with a slightly chitinized apical hood, and extending almost the length of the basal foramen beyond the basal tip.

Crioceris asparagi (Linnaeus) (Pl. 1, Figs. 4a, b)

Aedeagus tubular and curved. Its apex blunt and divided into two broad lobes. Apical orifice almost terminal. Basal foramen about one-third the length of the aedeagus, its anterior margin recurved and forming a pocket. The tegmen Y-shaped with a large keel-like strut possessing a tooth on its dorsal margin. (A spiculum gastrale was not found although several specimens were examined carefully for this particular structure. If present, it must be very small and closely attached to the genital pocket.) Internal sac short; a narrow, median dorsal plate and a prominent lateral plate at each side of the orifice.

Lema trilineata (Olivier) (Pl. 1, Figs. 5a, b)

Aedeagus considerably curved with its diameter the least in its mid-section; the floor posterior to the middle sharply bent downward to form the prominent anterior border of the basal foramen. The latter occupying approximately the anterior third of the ventral surface. Apex pointed with its tip curved slightly upward. The tegmen Y-shaped with an elongated keel which curves upward at the anterior. Internal sac approximately one-half the length of the aedeagus; broad median dorsal plate which bends ventrally into the orifice and then anteriorly to form laterally curved projections in the upper wall of the sac; a ribbon-like lateral plate on each side of the orifice, similar to but not so prominent as those in *Crioceris*.

Antipus laticlavata (Forster) (Pl. 1, Figs. 6a, b, c)

Aedeagus slightly curved; apical orifice large, approximately one-third the length of the aedeagus, its lateral walls sloping gradually toward the pointed apex. Floor of the orifice with median groove. Basal foramen large but less than one-half the length of the aedeagus. Tegmen Y-shaped with small lateral forks and a much broadened strut which almost completely fills the foramen and is truncated at the tip. The spiculum gastrale Y-shaped and composed of much flattened but rather heavily chitinized elements. The internal sac very short, complexly folded, and with chitinized ribbon-like plates at the orifice. A slender chitinous flagellum extending into the sac from its closed end.

Megalostomis subfasciata (Leconte) (Pl. 2, Figs. 7a, b, c)

Aedeagus broad, the basal half the broader; slightly curved. Apex flattened in a horizontal plane and truncated at the tip. Lateral walls of the orifice with a distinct lobe projecting posteriorly; a distinct notch below each lobe. Two groups of hairs on each lobe, the smaller group attached to the inner border dorsal and anterior to the tip, the larger group on the outer surface of its lower corner. The basal foramen approximately one-half the length of the aedeagus. Tegmen Y-shaped, the lateral forks curving upward and anteriorly,

the strut broad, slightly elevated in the median line and practically filling the foramen. Spiculum gastrale Y-shaped, composed of rather heavy rod-like elements; the strut approximately twice as long as the lateral forks and only faintly showing a fusion line of its component parts; ends of the lateral forks blunt. A broad, slightly bilobed, apical hood present. The internal sac, below the apical hood, heavily chitinized and tapering to surround a small opening at the posterior. A slender chitinized plate extends posteriorly and towards the median line along each side of the pointed portion. A large ribbon-like lateral plate extends posteriorly on each side from near the prominent lobe of aedeagus, curves toward the median line, then anteriorly and ventrally toward the interior of the aedeagus.

Babia quadriguttata (Olivier) (Pl. 2, Figs. 8a, b, c)

Aedeagus with much the same appearance from the lateral view as *Megalostomis* but slightly more curved. Apex tapering quickly to a rather blunt point. The apical orifice almost terminal in position. A group of long hairs attached to the inner border of the apical orifice slightly above the middle. The basal foramen two-thirds the length of the aedeagus. Tegmen Y-shaped with fairly broad lateral forks curving upward and with a broad strut tapering toward a truncated tip and roundly elevated in the median line. The spiculum gastrale Y-shaped, possessing an anterior keeled strut and pointed lateral forks. Walls of the internal sac more chitinized throughout and with chitinized plates extending into the orifice and consisting of the following: (a) two flattened dorso-lateral plates below which the membrane curves anteriorly and posteriorly bearing a (b) broad median apical hood with diagonal projections which connect anteriorly with (c) chitinized lateral plates near the lateral wall of the orifice.

Urodera crucifera Lacordaire (Pl. 2, Figs. 9a, b, c)

Aedeagus somewhat dorsoventrally flattened, broader at the posterior, and very slightly curved. Apical orifice almost terminal with two groups of hairs on its lateral borders; the more ventrally situated group of small hairs attached to the outer surface, the longer hairs more dorsal and on the inner surface of the orifice wall. The apex with a broad squared point, intermediate in width between *Megalostomis* and *Babia*. Tegmen Y-shaped with rather heavy lateral forks curving dorsally and anteriorly and with a broad strut truncated at the tip. Spiculum gastrale more triangular than Y-shaped, with the membrane chitinized between its lateral forks but with an elongated keel-like strut. Internal sac at orifice similar to *Urodera crucifera* in having dorso lateral and lateral plates and an apical hood chitinized. The chitinization of sac walls similar in general to *Urodera*.

Saxinis omogera Lacordaire (Pl. 2, Figs. 10a, b, c)

Aedeagus broader at apical portion and with considerable ventral curvature approximately one-fourth from the tip, the remaining three-fourths with little curve of ventral surface. Apical orifice almost terminal with an irregular row of long hairs attached to the upper inner surface of each lateral wall. Apex

slender, bluntly pointed and with a ventrally curved tip. Basal foramen large, approximately three-fourth the length of the aedeagus. Tegmen Y-shaped with posteriorly curved tips and a flattened strut, crudely truncate at its tip. Spiculum gastrale small with lateral forks barely shorter than the strut which is slightly keeled. The walls of the internal sac rather well chitinized throughout; a pair of curved dorso-lateral plates at the orifice beneath which are other complexly looped chitinous plates. No distinct apical hood present.

Exema conspersa var. *dispar* Lacordaire (Pl. 2, Figs. 11a, b, c)

Aedeagus considerably curved with posterior margin of the basal foramen chitinized and projecting abruptly downward anterior to the middle; a prominent hump directly above on the dorsal surface. The apical portion gradually tapering to a rounded and ventrally curved tip; its ventral surface supplied with hairs anterior to the tip. The basal foramen less than half the length of the aedeagus. Tegmen Y-shaped with rather heavy lateral forks and with a strut, much narrower than in *Saxinis*, elevated in the median line and rounded at the anterior. Spiculum Y-shaped with forks shorter than the strut which is slightly keeled at the anterior. A median dorsal plate present, its under fold forming a dorsal thickening in the wall of the sac. The closed end of the sac chitinous and boxlike through which a slender flagellum passes.

Griburius equestris (Olivier) (B) (Pl. 3, Figs. 12a, b, c)

Aedeagus broader at posterior half and with a rather marked ventral curve one-fourth of the distance from the distal end. The lateral walls of the apical orifice sloping gradually to the rather narrow truncated point; a group of long hairs on each side of the under surface of the apex anterior to the tip. Basal foramen large, approximately one-half the length of the aedeagus; the anterior border rather heavily chitinized but not with abrupt ventral curve. Tegmen Y-shaped with dorso-anteriorly curved forks and a large strut elevated in the median line; its tip pointed and curved upward toward the posterior giving a bilobed appearance. Spiculum with lateral forks much shorter than the strut; the latter quite rod-like and exhibiting greater fusion of its component elements. Opening of the internal sac large; the walls of the sac supported by looped dorso-lateral plates (lp); one on each side, which almost touch in the median line at the posterior, with a strap-like thickening in the median line of the ventral wall, a slender dorsal plate (dp) in the median line above the posterior ends of the dorso-lateral plates. The closed end of the sac pointed and extending posteriorly; its ventro-lateral portion with an elongate plate, ejaculatory guide, on each side.

Pachybrachis luridus (Fabricius) (B) (Pl. 3, Figs. 13a, b, c)

Aedeagus with posterior two-fifths broader and rather sharply curved ventrally. Apical orifice more terminal. Apex broad and tapering toward a rounded point; its side walls somewhat elevated to form a broad groove and its undersurface possessing groups of hairs, two lateral and one medio-posterior near tip. Basal foramen large, over half the length of the aedeagus. Tegmen

Y-shaped and with a large strut elevated in the median line, similar to that of *Griburius*. Spiculum rather long and Y-shaped; its lateral forks broad at their bases and much shorter than the more slender strut of firmly fused parts and with its anterior tip keeled and curved ventrally. A rather broad median dorsal plate, a pair of dorso-lateral plates and a median ventral plate in the walls of the sac at the orifice.

Monachulus saponatus (Fabricius) (B) (Plate 3, Figs. 14a, b, c)

Aedeagus small, broad and feebly curved. The lateral walls of the orifice curving ventrally and then posteriorly to form distinct rounded notches at the sides. Apex broadly truncate and under surface with a group of hairs on each side anterior to the tip. Basal foramen approximately one-half the length of the aedeagus. Tegmen Y-shaped with short forks curving dorso-posteriorly and with a large strut, broad and slightly elevated in the median line. Spiculum Y-shaped and composed of rod-like elements; its lateral forks pointed at the tips and shorter than the bluntly tipped strut. Internal sac extending anteriorly to middle of foramen; a broad dorsal plate at the orifice beneath which a pair of irregular lateral plates extends posteriorly toward the median line.

Cryptocephalus leucomalis Suffrian (Pl. 3, Figs. 15a, b, c)

Aedeagus abruptly curved ventrally one-third from the posterior and continuing in a more or less horizontal plane toward the narrowly truncated tip; the latter slightly curved ventrad. Under surface of apex supplied with hairs anterior to the tip. Ventral surface near the mid-section curves slightly to form the posterior border of the large basal foramen. Tegmen Y-shaped with short dorsally curved forks and with a large strut elevated in the median line. Spiculum Y-shaped with a keeled strut. The internal sac long, chitinous and box-like at the orifice; a chitinous apical hood in the median line with a pair of lateral rounded lobes at its posterior which extend downward almost to the apical tip; a pair of looped lateral plates supporting the sides of the sac at the orifice.

Chrysodina globosa (Olivier) (Pl. 3, Figs. 16a, b)

Aedeagus elongate with a deep transverse depression in its dorsal surface slightly posterior to the middle; more heavily chitinized posterior to the depression and sharply curved ventrad. Apical orifice caudad. Apex broadly truncate with corners turned slightly ventrad. Basal portion of aedeagus shallowly convex above with rod-like thickenings along the lateral borders. Basal foramen over half the length of the aedeagus; its posterior border sharply bent ventrad, heavily chitinous at the sides forming lateral vertical grooves on its anterior face. Tegmen Y-shaped with its struts nearly continuous above the aedeagus in the median line; its strut broad and flat, roundly pointed at the tip. Internal sac one-half longer than the aedeagus, its walls generally membranous throughout; just inside the orifice supplied with chitinous plates of complex structure. A pair of roughly thickened and rod-like ejaculatory guides arising within the sac near the middle of the aedeagus and extending posteriorly to bend upward anterior to the orifice.

Colaspis brunnea (Fabricius) (Pl. 3, Figs. 17a, b, c)

Aedeagus of same general form as in *Chrysodina globosa*, but having a more pronounced general curve; the transverse depression of dorsal surface farther anterior and more rounded at bottom; a distinct but short transverse dorsal ridge across the median line just posterior to the transverse depression; posterior portion heavily chitinized from the depression and curved ventrad. Apical orifice larger, extending farther anteriorly; its posterior edge elevated anterior to the apex. The latter bluntly pointed and with slight dorsal curve. The basal portion of the aedeagus more convex with lateral rod-like thickening higher on sides than in *Chrysodina*. Ventral floor of the aedeagus sharply curved ventrad at the posterior border of the basal foramen as in the preceding species but with deeper vertical grooves at the sides of its anterior face. Tegmen Y-shaped with broad strut ending in sharp point at the anterior. Spiculum small with lateral forks stouter at their bases, pointed at tips, and approximately the same length as the strut; the latter sharply bent ventrad near its slender and pointed anterior end. Internal sac, approximately one and one-half the length of the aedeagus, with walls membranous in anterior portion; posterior portion box-like, with a pair of dorso-lateral plates and a lateral plate at each side below, all of which may be protruded from the orifice.

Colaspis brunnea var. *costipennis* Crotch

Structures the same as in *C. brunnea* except the apex appears to have a slightly greater upward curve.

Rhabdopterus picipes (Olivier) (Pl. 4, Figs. 18a, b, c)

Aedeagus, in general, similar to the preceding; transverse dorsal depression pronounced but narrower; dorsal transverse ridge more elevated. Apex tongue-like, fairly broad and with rounded tip. Posterior edge of apical orifice elevated as in *Colaspis*. Basal foramen approximately two-thirds the length of the aedeagus; its margin similar to that of *Colaspis*. Anterior portion of the aedeagus less heavily chitinized than the posterior; a rod-like support in the wall above each lateral edge; a thin but pronounced keel in the median line of the dorsal surface; a slight cleft at the extreme anterior end. Tegmen Y-shaped with lateral forks slender, pointed, somewhat S-curved, nearly meeting in mid-dorsal line above aedeagus. Spiculum small with curved and pointed forks and a very small strut. Internal sac much longer than aedeagus and generally membranous throughout; a pair of dorso-lateral plates present at the orifice.

Xanthonia villosula (Melsheimer) (Pl. 4, Figs. 19a, b, c, d)

Aedeagus with apical third bent almost at right angle to the remainder; apex broadly flattened, with upward curve and with two elongated and bluntly pointed lobes, the latter angling toward their respective sides and separated by a deep rounded notch. Anterior portion of the aedeagus above the basal foramen, broad and roundly convex with somewhat flattened margins; its mid-dorsal line distinctly keeled. Basal foramen approximately one-half the length

of the aedeagus; its posterior margin chitinous, but not vertically grooved at its lateral corners. Transverse dorsal depression and dorsal ridge not present. Tegmen crudely H-shaped; its lateral forks slender and almost joining in median line above aedeagus; strut broader than the aedeagus with its anterior extremity very broadly and distinctly bilobed. Spiculum Y-shaped; lateral forks pointed and with upward curve; strut slightly keeled at anterior. A secondary spiculum (?), crudely triangular in shape, with an elongated and sharply pointed strut present. Internal sac long with a slender median and a pair of lateral plates at orifice.

Fidia viticida Walsh (Pl. 4, Figs. 20a, b, c)

Aedeagus with posterior two-fifths bent at right angle to remainder; apex slightly flattened with two short, broad and bluntly pointed lobes separated by a widely rounded notch; anterior portion quite convex, broader than the posterior and with a slight keel anteriorly in the median line. Similar to *Xanthonia* in not having transverse depression and dorsal ridge in the middle region. Basal foramen approximately one-half the length of the aedeagus, its posterior margin curved rather abruptly ventrad but not vertically grooved at junction with side margins. Tegmen crudely H-shaped with small lateral forks and a broad strut, elevated slightly along lateral margins and broadly bilobed at the anterior. Spiculum Y-shaped, its strut longer than lateral forks and slightly keeled at the tip. Internal sac longer than aedeagus with a narrow dorsal plate in the median line and a pair of chitinous lateral plates at the orifice; several pairs of broad curved plates within the sac in mid-section of aedeagus.

Metachroma parallelum Horn (B) (Pl. 4, Figs. 21a, b, c, d)

Aedeagus with similar curvature and form as in *Fidia viticida*; apex broad with three terminal lobes, a broadly rounded one on each side separated by a deep notch from a longer and sharply pointed lobe in the median line. Anterior portion slightly more heavily chitinous than in *Fidia*; slightly keeled anteriorly in the median dorsal line. Basal foramen less than one-half the length of the aedeagus; its posterior margin chitinous, antero-ventrally projected and without vertical grooves at junction with side margins. Tegmen H-shaped and mostly heavily chitinized; lateral forks pointed and curved anteriorly at tips; strut wider than the aedeagus and broadly bilobed at the anterior. Two distinct spicula present; the larger, primary, one in normal position, heavy and Y-shaped with stout strut barely longer than lateral forks and with small keel at tip; the secondary one, ventral to the primary and smaller, stout and Y-shaped. Internal sac longer than aedeagus, its walls generally membranous throughout; a pair of thinly chitinous lateral plates at the orifice. A pair of small chitinous rods within the sac anterior to the orifice.

Adoxus obscurus (Linnaeus) (Pl. 4, Figs. 22a, b, c, d)

Aedeagus with posterior two-fifths curved ventrad, almost at a right angle; apex flattened and slightly broader than aedeagus at orifice; a thickened triangular piece in the median line with its basal angles slightly beyond the general

posterior edge of the aedeagus and possessing a groove at the posterior junction of the lateral edges of the orifice; the posterior corners of the apex much flattened, roughly rounded and slightly bent antero-ventrad. Basal foramen approximately one-half the length of the aedeagus; its posterior border chitinous and projecting antero-ventrally. Aedeagus widest at basal portion with convex surface chitinous but with lateral and anterior edge less so. Tegmen H-shaped, similar to that in preceding species. Two spicula present; the primary (larger) one Y-shaped with tapering forks and long but rather stout strut; the secondary (smaller) one also generally Y-shaped with lateral forks very widely separated at its pointed tips and a short stout strut ending in two sharp points. Internal sac much longer than aedeagus and with a roughly triangular opening at orifice guarded or supported by chitinous plates.

Glyptoscelis pubescens (Fabricius) (Pl. 5, Figs. 23a, b)

Aedeagus large with apical fourth bent sharply ventrad; wide but shallow depression in mid-section of dorsal surface. Apex sharply pointed. A broad and shallow depression on under surface between the ventrally curved portion and the posterior border of basal foramen; the border very prominent, chitinous and projecting ventrally, somewhat cupped at sides. Basal foramen over one-half the length of the aedeagus; extreme anterior margin with triangular cleft in the median line. Tegmen Y-shaped with small and sharply pointed lateral forks and a large broad strut, two-thirds the length of the basal foramen, elevated in the median line, and ending in a rather sharp point at anterior. Internal sac longer than aedeagus, its walls generally membranous but with a pair of lateral plates at the orifice; sac opening large and rounded.

Colaspidea varicolor Crotch (Pl. 5, Figs. 24a, b, c, d)

Aedeagus smaller than in *Glyptoscelis* but of same general character; sharply curved at mid-section, posterior portion almost at right angle to basal section; no transverse dorsal impression. Apical portion flattened above and slightly asymmetrical with right lateral wall of orifice longer and more curved. Apex small with blunt tip. Basal foramen large but less than half the length of the aedeagus; its posterior border curving ventrally and anteriorly but without the lateral cups or grooves as in *Glyptoscelis*; its extreme anterior edge cleft in the median line. Tegmen H-shaped with slender lateral forks and a broad strut with two sharply pointed lobes at the anterior. Spiculum Y-shaped with slender lateral forks barely shorter than the stouter strut; the latter showing almost throughout its length the fusion line of its component elements. A T-shaped structure, probably a secondary spiculum, with broadly flattened crossbar and a rod-like upright with pointed anterior tip beneath the spiculum. Internal sac longer than aedeagus with walls generally membranous; a crudely V-shaped lateral plate on each side of the sac at the orifice. A pair of chitinous rods, one at each side of the lateral line within the sac posterior to the orifice.

Typophorus viridicyaneus (Crotch) (B) (Pl. 5, Figs. 25a, b, c)

Aedeagus large with ventrally curved posterior portion less than one-half

the length of the aedeagus. Apical portion constricted at posterior to form a small, median and upward curved point; its upper surface in the orifice with slight groove in the median line. Floor of aedeagus at posterior border of foramen similar to *Colaspidea* but with broader lateral walls. Basal foramen approximately one-half the length of the aedeagus; its anterior border especially thinly chitinized. Tegmen H-shaped with short and slender lateral forks, more ventral in position; its strut broader than the aedeagus above it and with two large squarely tipped lobes at the anterior. Lateral margins and a flat ridge in the median line elevated. Spiculum stout and Y-shaped with a strut slightly keeled at the extreme anterior and in the dorsal line. Internal sac longer than the aedeagus and mostly membranous; at orifice strengthened by a chitinous lateral plate on each side and with a flattened dorsal plate at each side of median line in its dorsal fold.

Chrysochus auratus (Fabricius) (Pl. 5, Figs. 26a, b, c)

Aedeagus large with posterior portion bent sharply ventrad about one-third from tip of apex; apical portion tapering sharply to a rather long upturned tip. Basal portion with slight keel in median dorsal line. Basal foramen approximately one-half the length of the aedeagus; its posterior border similar to *Glyptoscelis* with posteriorly and slightly laterally projecting ridge on its posterior surface. Tegmen Y-shaped with lateral forks broad and flat, almost joining above the aedeagus; its strut broad at base but tapering toward a single point at the anterior. Spiculum small, chitinous, and crudely Y-shaped; its lateral forks forming acute angles with the strut which projects slightly posterior to the junction. Internal sac generally membranous and approximately the length of the aedeagus; a bifurcated dorsal plate at the orifice; a spirally twisted plate extending into the sac at its closed end.

Chrysochus cobaltinus Leconte (Pl. 5, Figs. 27a, b, c)

Aedeagus very similar to that of *C. auratus* but larger; apical tip shorter; lateral ridges on posterior border of basal foramen more posteriorly curved and with narrower lateral walls. Tegmen similar but with thin lateral margins to tip of the strut. Spiculum small, almost T-shaped. Internal sac shorter than the aedeagus and with smaller bifurcated dorsal plate at the orifice; a spirally twisted plate inside the sac similar to that in the preceding species.

Timarcha intricata Haldeman (Pl. 6, Figs. 28a, b)

Aedeagus large and curved; apex somewhat flattened, broadly rounded at tip; orifice less than one-fourth the length of the aedeagus. Basal foramen occupying more than one-third of the ventral surface. Dorsal surface of basal portion deeply cleft above the foramen, with a small lobe on the median edge of each lateral piece at the extreme anterior. Tegmen ring-like with broad, single lobed tegmental cap tipped with hairs; heavy lateral forks connect the cap with the stout rod-like strut below. Spiculum observed to be V-shaped, stout, and large. Internal sac long and, at repose, extending anteriorly through the dorsal cleft of the basal portion of the aedeagus; a broad median dorsal plate at the orifice. An elongated but stout flagellum present inside the sac.

Entomoscelis adonidis (Pallas) (Pl. 6, Figs. 29a, b, c)

Aedeagus large with basal portion sharply bent downward approximately one-fourth from the anterior; apical orifice large, its lateral walls sloping gradually to a square pointed tip; each lateral wall flattened from above and presenting a lobe, directed toward the median line, posterior to the middle of the orifice. Basal foramen small, occupying approximately one-fourth of the ventral surface of the aedeagus; its lateral walls broadened in a vertical plane, presenting a posterior as well as a ventro-anterior edge. Tegmen V-shaped with slender pointed lateral forks and its anterior portion curved sharply anterior at an angle with the forks. Spiculum Y-shaped, approximately two-thirds the length of the aedeagus; its strut showing the rod-like elements throughout its length. Internal sac shorter than aedeagus with a short median dorsal and a pair of lateral plates at the orifice. (No observations on the flagellum were made.)

Prasocuris vittata (Olivier) (Pl. 6, Figs. 30a, b, c)

Aedeagus small with slight curve; apical orifice large; apex roundly pointed. Basal portion with small cleft in the median line at the anterior. Basal foramen more than one-third the length of the aedeagus; its lateral margins sinuate. Tegmen Y-shaped and stout with lateral forks curved sharply upward nearly forming right angles with the strut; the latter slightly keeled at anterior tip. Spiculum V-shaped; lateral forks slender and rod-like; strut, if present, tiny. Internal sac approximately one-half the length of the aedeagus with a dorsal plate at the orifice. A chitinous flask-like flagellum with pointed tip present inside the sac.

Labidomera clivicollis (Kirby) (Pl. 6, Figs. 31a, b, c)

Aedeagus large and with rather regular curve; apex more sharply curved ventrad, with broad shallow depression on mid-ventral surface, and tapering to a blunt point. Basal portion with a rounded elevation at the anterior border. Basal foramen approximately one-third the length of the aedeagus. Tegmen V-shaped, of moderate size but stout; its lateral forks tapering to pointed tips. Spiculum large, approximately two-thirds the length of the aedeagus, presenting an elongate V-shape, somewhat twisted, and with the right fork slightly longer than the left. Internal sac almost as long as the aedeagus with a membranous dorsal fold at the orifice beneath which the distal end forms a slender tube surrounding a slender flagellum. The latter with sharp ventral curve anterior to the tip; the tip sharp pointed, curved dorsally, and protruding into the orifice in repose. (The material of this species consisted of pinned specimens only. The aedeagus of each when found was lying on its left face with the anterior portion of the spiculum along its dorsal face and one fork of the latter beneath it. While no fresh material has been examined by the author he feels that because of its weight this must be the natural position of the aedeagus in repose. The twisting of the aedeagus in this manner could well be responsible for the asymmetry of the spiculum.)

Labidomera clivicollis var. *rogersi* Leconte

Aedeagus with same general form as the typical species but slightly smaller

in size. The tegmen and spiculum of the same general form but composed of slightly less stout elements.

(Beetles of the above variety were smaller than the typical species, accounting for the difference in size of the genitalia.)

Leptinotarsa rubiginosa (Rogers) (Pl. 6, Figs. 32a, b)

Aedeagus large, cylindrical, and rather regularly curved; apical orifice small; apex bluntly pointed and slightly asymmetrical; a broad and shallow groove in the mid-ventral surface from below anterior of the orifice to the posterior border of the basal foramen. Basal portion short with basal foramen less than one-fourth the length of the aedeagus. Tegmen small and V-shaped; its rod-like elements slender and pointed at their distal ends; the anterior portion, corresponding to the strut, short and sharply bent anteriorly. Internal sac extending anteriorly beyond the posterior edge of the basal foramen; a membranous dorsal fold at the orifice stiffened on each side by a chitinous plate. The flagellum stout and somewhat bulbous at the juncture with the internal sac at the anterior.

Leptinotarsa haldemani (Rogers) (Pl. 7, Figs. 32a, b, c)

Aedeagus large and in general similar to *L. rubiginosa* but with less diameter anterior to orifice; apex shorter with lateral surfaces more rounded; basal portion not so sharply curved ventrad with basal foramen occupying nearly one-fourth of the ventral surface of the aedeagus. Forks of the tegmen heavier, blunt, pointed, and more widely separated at the anterior. Spiculum about three-fourths the length of the aedeagus forming an elongated V, the lateral elements almost touching for over half their length; its position and asymmetry similar to that in *Labidomera*. Closed end of internal sac extending into the basal foramen; a lateral plate on each side at the orifice. Flagellum heavily chitinized, elongate, and with a bulbous enlargement at its base.

Leptinotarsa lineolata Stål (Pl. 7, Figs. 34a, b, c)

Aedeagus small, dorso-ventrally flattened in apical region; apical floor elongate, rounded at tip and with deep groove on its dorsal surface in median line. Apical orifice large with low side walls, irregular on their dorsal edge. Mid-section of the ventral surface of aedeagus with wide shallow depression. Basal portion with a broad lobe in the median line of its anterior border. Tegmen stout and V-shaped; its anterior portion with sharp upward curve a short distance from its extremity. Spiculum more than two-thirds the length of the aedeagus; composed of two elongated rods, more widely separated throughout their length than in *L. haldemani* but presenting a general V-form. Anterior end of the internal sac protruding into the basal foramen; a broad but membranous dorsal fold at orifice. The flagellum heavily chitinized and with an enlargement at its base.

Leptinotarsa decemlineata (Say) (Pl. 7, Figs. 35a, b, c)

Aedeagus large, not so large as in *L. rubiginosa* and *L. haldemani* but of same general character; the ventral surface with more rounded curve through-

out; lateral surfaces of apex straight, much as in *L. rubiginosa*, but converging to a narrower truncated point at tip; ventral surface shallowly grooved in the median line. Basal foramen approximately one-third the length of the aedeagus; the lateral and dorsal margins not cupped at the extreme anterior but forming a roundly curved roof. Tegmen V-shaped and stout; its lateral forks separated at the anterior and joined by a transverse bar which is bent dorsally into the foramen. Spiculum asymmetrical, twisted, and with an elongated V-shape; its lateral elements narrowly separated for approximately half their length and joined at their anterior ends. Position of spiculum similar to that of *L. haldemani* (not so shown in Figure 35b). Internal sac extending anteriorly to beyond the posterior margin of the foramen; slender lateral plates at the sides of a membranous dorsal fold at the orifice. The flagellum stout with a funnel shaped tip; when retracted usually protruding into the orifice.

Zygogramma exclamationis (Fabricius) (Pl. 7, Figs. 36a, b, c)

Aedeagus of medium size and with slight general curve; apex nearly as broad as aedeagus at the orifice; its posterior edge flattened, curved ventrally, and at each corner possessing a lateral lobe, sharply pointed and bent antero-ventrally. Ventral surface of the apical portion grooved in the median line. Basal foramen approximately one-third the length of the aedeagus. Tegmen V-shaped with the anterior end curled upward into the foramen. Spiculum Y-shaped and slightly less than two-thirds the length of the aedeagus; its lateral elements rather widely separated at the posterior but barely separated anteriorly over two-thirds of its length. Internal sac generally membranous throughout and extending anteriorly beyond the posterior border of the basal foramen; its posterior extremity chitinous and forming a short broad sheath about the tip of the stout flagellum.

Zygogramma continua Leconte (Pl. 8, Figs. 37a, b)

Aedeagus similar to that in *Z. exclamationis*; not so stout throughout and more flattened at the apical half; posterior edge of apex more sharply curved, slightly longer in the median line; its lateral corners, smaller and more sharply bent toward the anterior. Basal foramen approximately one-third the length of the aedeagus; narrower at anterior than at posterior. Tegmen slightly more U- than V-shaped, the lateral elements more widely spread at the anterior. Internal sac membranous extending anteriorly beyond posterior margin of the foramen; at the orifice its posterior extremity forming a tubular chitinous sheath for the stout flagellum.

Zygogramma suturalis var. *casta* Rogers (Pl. 8, Figs. 38a, b, c)

Aedeagus similar, in general, to that of *Z. continua* but smaller and with greater diameter in its mid-section. The apex more elongate and with its lateral margins nearly parallel anterior to the lateral points; the posterior border more angulate than in *Z. continua* and with the lateral points less sharply curved toward the anterior. The basal foramen less than one-third the length of the aedeagus; its posterior border lightly chitinized. Tegmen V-shaped, similar to that of the preceding species. The spiculum Y-shaped and quite symmetrical. Internal sac short and generally membranous throughout.

Flagellum slender and pointed at the lower margin of its tip; usually protruding into the orifice when retracted.

Zygogramma disrupta Rogers (Pl. 8, Figs. 39a, b, c)

Aedeagus and tegmen of the same general form as in the preceding species of this genus. The apex more flattened and more elongate in the median line; its posterior border angling more acutely toward the prominent lateral points than in *Z. suturalis casta*; the lateral margins curving outward anterior to the lateral points. Tegmen similar to that of other species of the genus. The spiculum of similar form as the preceding but slightly asymmetrical. Internal sac, when retracted, barely reaching the posterior margin of the foramen. A stout flagellum, not pointed, present.

Calligrapha lunata var. *hybrida* (Say) (Pl. 8, Figs. 40a, b, c)

Aedeagus quite similar to that of *Zygogramma exclamationis*; the apex generally broader than in the latter, its posterior border more roundly curved and with smaller lateral points; the sides of the aedeagus more curved at the orifice and its basal region narrower. Tegmen V-shaped and stout. Spiculum more V-shaped, slightly asymmetrical and stouter toward its posterior tips. Internal sac when retracted almost reaching posterior border of foramen and forming a tubular sheath about the flagellum at the orifice. The flagellum slender with a small sharp point on each side of its tip.

Calligrapha similis Rogers (Pl. 8, Figs. 41a, b, c)

Aedeagus slightly smaller than the preceding one and showing greater curvature. The apex with sides nearly parallel from the orifice to the lateral points; a prominent rounded lobe in the median line of the posterior border. The basal foramen small, less than one-third the length of the aedeagus. Tegmen similar to that in the preceding species. The spiculum Y-shaped and quite symmetrical. Flagellum stout but tapering toward the tip; the latter bifurcated, a slender but irregular rod-like element on each side curving outward from the median line.

Calligrapha praececlsis Rogers (Pl. 9, Figs. 42a, b, c)

Aedeagus larger and more heavily chitinized than in the preceding species of this genus; the lateral view of the aedeagus and flagellum very similar to those of *Labidomera clivicollis*. The apex tapering toward a single blunt point. Basal foramen slightly more than one-third the length of the aedeagus; a rounded cleft in the median line of its anterior border. The tegmen V-shaped but longer and with a more pointed anterior end than in any other species of this genus. The spiculum much heavier and longer, nearly equal to the length of the aedeagus; very similar to those in the species of *Labidomera* and *Leptinotarsa*. The internal sac comparatively short and usually protruding into the orifice. The flagellum quite slender and tapering gradually toward its tip; the latter enclosed in a slender sheath from the internal sac.

Calligrapha elegans (Olivier) (Pl. 9, Figs. 43a, b, c)

Aedeagus and tegmen very similar to those of *C. similis*. Lateral corners of the posterior border of the apex not sharp, but rounded; the median lobe of the posterior margin longer and narrower. The spiculum slightly more V- than Y-shaped and quite symmetrical. A pair of slightly thickened strips (1p), laterally placed, in the dorsal wall of the sac above the orifice. Flagellum stout, somewhat irregular in diameter, and with a divided tip similar to that in *C. similis*; the lateral elements resembling a pair of sharply bent fishing hooks, each with its point directed toward its respective side.

Calligrapha scalaris Leconte (Pl. 9, Figs. 44a, b, c)

Aedeagus somewhat similar to that of *C. lunata hybrida* but with greater curvature. The apex broader posterior to the orifice; slightly longer in the median line with posterior border angling and then curving anteriorly toward the prominent lateral points. Tegmen and spiculum similar to those in *C. lunata hybrida*; the latter part longer and lighter toward its tips. Flagellum stout, possessing an expanded funnel-shaped tip with a deep V-cleft above. The tip partly covered by a sheath from the internal sac.

Calligrapha spirea (Say) (B) (Pl. 9, Figs. 45a, b, c)

Aedeagus with less curvature than in *C. scalaris* but very similar in form and size. The posterior border of the apex a broad somewhat undulated curve, most posterior at the mid-point; the lateral points prominent but more curved toward the anterior and with less distance between them than in *C. scalaris*. Tegmen and spiculum similar to those in the latter species; the latter part also asymmetrical but with stouter elements of less curvature. Flagellum stout, rather broadly divided at its tips; each lateral part bearing a tuberculated dorso-caudal border.

Calligrapha multipunctata (Say) (Pl. 10, Figs. 46a, b, c)

Aedeagus with form and size very similar to that of *C. lunata hybrida* but with greater depth in the mid-section and higher lateral walls at the orifice. The apex broader; its lateral points farther apart; the posterior margin with a slight anterior dip in the median line. The tegmen V-shaped, of lighter elements, and with its anterior portion sharply curved upward. The spiculum V-shaped and with the right fork longer. The flagellum quite stout with a sharp point at each side of the tip.

Calligrapha bigsbyana (Kirby) (Pl. 10, Figs. 47a, b, c)

Lateral view of the aedeagus similar to that of *C. multipunctata*; its depth in the mid-section less than in the latter and the lateral walls of the foramen not curved upward at the anterior; the length slightly greater. The apical portion above very similar to that of *C. scalaris* and *C. spirea*; the posterior border a broad rounded curve with a slight undulation at each side of the middle and with prominent lateral points. The anterior extremity of the aedeagus more truncate than rounded. Tegmen V-shaped, similar to that of *C. scalaris*. The

spiculum Y- or almost V-shaped, more than two-thirds the length of the aedeagus; its right fork approximately one-fourth longer than the left. Flagellum stout, enlarging just anterior to its bifurcated tip; the side elements of the latter more widely separated at their points and tuberculate on their outer borders.

Calligrapha sigmoidea Leconte (Pl. 10, Figs. 48a, b, c)

Aedeagus and tegmen very similar in size and form to that of *C. bigsbyana*. Sides of the apical portion continuing almost parallel to the prominent lateral points of the posterior border; the latter more rounded than in the preceding species. Spiculum Y-shaped, quite symmetrical; approximately three-fourths the length of the aedeagus. Flagellum stout, similar to that of *C. bigsbyana*; its tip more widely cleft at the posterior; its lateral surfaces not tuberculate.

Calligrapha serpentina Rogers (Pl. 10, Figs. 49a, b, c)

Aedeagus large and of the same general form as *C. sigmoidea*. The lateral walls at the orifice higher and their upper margins curving sharply ventrad at the posterior; almost parallel but with a slight curve toward the median line between the middle of the orifice and the lateral points. The anterior end of the aedeagus more rounded. Tegmen V-shaped. Spiculum also V-shaped, long, and slightly asymmetrical. Flagellum stout with a large funnel-shaped tip, widely cleft below.

Chrysolina (= *Chrysomela* auth.) *flavomarginata* (Say)
(Pl. 10, Figs. 50a, b, c)

Aedeagus much curved below, bending more sharply ventrad one-third from the posterior tip. The sides of the apex tapering toward a single blunt point at the posterior; the undersurface with an upward curve. Basal foramen approximately one-third the length of the aedeagus. Tegmen V-shaped. The spiculum Y-shaped and quite symmetrical; the lateral elements rather widely separated just posterior to their junction but contiguous at their mid-sections. The internal sac short and generally membranous. The flagellum curved and slender, tapering toward a sharp point at the posterior; in all specimens observed, lying in a narrow groove in the median line of the apical floor and protruding posteriorly beyond the aedeagus.

Chrysolina (= *Chrysomela* auth.) *cribraria* (Rogers) (B)
(Pl. 11, Figs. 51a, b, c)

The aedeagus with shape, in general, similar to that of *Leptinotarsa rubiginosa*, but slightly smaller in size. Apex broadest at the region of the orifice, not pointed as in *C. flavomarginata*, and with rounded posterior border; the latter ending on each side of the orifice in lateral points; the points inconspicuous from above and directed toward the anterior. The orifice large. Basal foramen approximately one-third the length of the aedeagus. Tegmen V-shaped, showing the asymmetry observed in the larger species of *Leptinotarsa*. Flagellum elongated, curved downward and posteriorly, and gradually tapering to near its tip; the latter slightly expanded.

Chrysolina (= *Chrysomela* auth.) *montevagans* (Leconte) (B)
(Pl. 11, Figs. 52a, b, c)

Aedeagus similar to that of *C. cribraria* but smaller and with less curvature. The posterior border of the apex rounded but not extending so far anteriorly at the sides; the lateral points very inconspicuous and not seen from above. The orifice much smaller and not so rounded. Basal foramen at least one-third the aedeagus' length. Tegmen V-shaped, similar to that of the preceding species. Spiculum, large, quite symmetrical, and V- or Y-shaped; its lateral elements somewhat expanded near the tips. The flagellum slender, tapering toward the posterior tip; not so curved as in the preceding species of the genus.

Plagioderia versicolora (Laicharteg) (Pl. 11, Figs. 53a, b, c)

Aedeagus small; its undersurface considerably curved, undulating from anterior to posterior; its apex tapering gradually from the sides of the orifice to a broad single tip. The orifice partially covered by a rather broad apical hood; the sides of the latter bent downward near the junction with the upper wall of the aedeagus. The basal foramen more than one-third the length of the aedeagus; its anterior border deeply cleft in the median line. The tegmen forming a Y, all three extremities pointed. The spiculum of slender elements and almost U-shaped; approximately three-fourths the length of the aedeagus. The internal sac with a chitinous block at its closed end. The flagellum broad posterior to the block. A slender ejaculatory duct with a thistle-tube end projects into the flagellum.

Gastrophysa (= *Gastroidea* auth.) *polygoni* (Linnaeus) (Pl. 11, Figs. 54a, b)

Aedeagus small; its greatest width in the mid-section and approximately one-half its length; the posterior half narrowing slightly just posterior to the orifice; the posterior border curving from each side abruptly toward the median line to form a short rounded point. The upper surface of the apex with a deep and rather broad groove in the median line from the orifice to the posterior tip; the lateral margins of the groove elevated in sharp ridges. A broad apical hood, bilobed at the posterior and with its side margins bent downward, extends posteriorly above the orifice. Basal foramen large, almost one-half the length of the aedeagus; the anterior margin with a short narrow cleft in the median line. Tegmen Y-shaped, broadened at the junction of the forks and the strut; the latter slightly longer than the former and pointed at its tip. Spiculum not observed. The internal sac short with pairs of curved and looped plates near its closed end; a short tubular flagellum among the plates in the median line. A slender ejaculatory duct passes through the flagellum.

Gastrophysa (= *Gastroidea* auth.) *dissimilis* (Say) (Pl. 11, Figs. 55a, b)

Aedeagus and tegmen very similar to those of *G. polygoni*. Aedeagus larger and with a more prominently pointed apex. The median groove on the upper surface of the latter very narrow, extending only a short distance posterior to the orifice, and with thickened rolled borders. The apical hood broader, with its lateral margins almost parallel, and with a straighter posterior

margin. Basal foramen large; its anterior border cleft in the median line. No spiculum observed. The internal sac and the chitinous structures within it similar to those in *G. polygoni*, differing only slightly in details of size and arrangement of plates.

Gastrophysa (= *Gastroidea* auth.) *cyanea* Melsheimer (Pl. 12, Figs. 56a, b)

Aedeagus very similar in form to that of *G. dissimilis*, differing from the latter in having the groove of the apex longer, but narrow, and extending farther toward the posterior; the edges of the groove and the anterior border of the orifice rolled. Posterior border of the apical hood slightly anterior in the median line, barely forming two indistinct lobes. The anterior border of the basal foramen deeply cleft. The tegmen Y-shaped; its strut bent upward into the foramen and keeled at its tip. Spiculum not observed. The internal sac short; its internal structures varying only slightly in size and arrangement from those of the preceding species of the genus.

Chrysomela (= *Lina* auth.) *interrupta* (Fabricius) (Pl. 12, Figs. 57a, b, c)

Aedeagus large; its lateral view presenting a rounded curve above; the lower surface of the posterior portion and the lower border of the basal half forming a crude obtuse angle at the mid-section. The sides of the apical portion turning gradually toward the median line to form a broad rounded point at the posterior; the latter point slightly elevated. The basal portion of the aedeagus expanded, convex above, and with a deep cleft in the median line at the anterior. Basal foramen large, approximately one-half the length of the aedeagus. Tegmen Y-shaped, composed of flattened elements; its strut flattened from the sides. Spiculum delicate and roundly U-shaped. The internal sac barely extending anteriorly to the foramen; a pair of lateral plates above at the orifice; inner surface of the sac densely studded with tubercles. A short, sharply pointed flagellum present.

Chrysomela (= *Lina* auth.) *scripta* (Fabricius) (Pl. 12, Figs. 58a, b, c)

Aedeagus, tegmen and spiculum very similar in form to those in the preceding species. The aedeagus slightly smaller and more regularly curved toward the posterior on its lower surface; the sides of the apex curving more abruptly toward the median line and with greater height just anterior to the tip. The orifice more rounded. The basal portion convex and more expanded than in the mid-section; a cleft in the median line of the anterior border. The internal sac extending anteriorly almost to the foramen with its internal surface densely tuberculate. A short flagellum, curved and tapering to a short point, present in the closed end of the sac.

Trirhabda canadensis (Kirby) (Pl. 12, Figs. 59a, b)

Aedeagus quite large; its under surface with little curve except near the anterior end; the upper surface abruptly curved ventrad from approximately one-tenth from the anterior. The sides of the apex, posterior to the orifice, rather abruptly curving toward the median line to form a small point. The

orifice long and asymmetrical. Basal foramen small, almost wholly terminal; its lateral borders roundly notched at the posterior and with thickened rolled edge at the sides and anterior. Tegmen Y-shaped; the elongated strut laterally flattened and hooked upward at its anterior tip. No spiculum found. The internal sac much longer than the aedeagus; its diameter less in its anterior half which may be looped inside the aedeagus; its walls not tuberculate. A slender flagellum with a tip curved in a horizontal plane; the latter distinctly serrated on the outer side of the curve.

Erynephala (= *Monoxia* auth.) *puncticollis* (Say) (Pl. 13, Figs. 60a, b)

The aedeagus very long, slender and arched from below; more sharply curved downward near the posterior; its anterior end abruptly curved postero-ventrad. The upper surface of the posterior half somewhat dorsoventrally flattened but the anterior half more cylindrical. The apex elongated and constricted from the sides halfway between the orifice and the posterior tip to present a blunt arrow-head form. The orifice elongated and asymmetrical. Basal foramen small and quite terminal. Tegmen Y-shaped, the strut much longer than the small lateral forks and with a dorsal curve at its anterior tip. No spiculum observed. The internal sac much longer than the aedeagus, often looped inside the latter, but not possessing tuberculate walls within the main body of the aedeagus. The flagellum was not observed.

Diabrotica duodecempuncta (Fabricius) (Pl. 13, Figs. 61a, b, c)

Aedeagus large and with considerable arch from below; the curve presented by the lateral margin below broken by a wide angular drop in the posterior half of side wall of the foramen. The apical orifice slightly less than one-third the length of the aedeagus; its posterior two-thirds with low lateral walls. The posterior end of the aedeagus rounded at the sides and posteriorly below; above forming three points, the lateral ones curved toward the median line and separated by depressions from the broader median point which extends beyond the remainder of the posterior margin. A large roughly oval apical hood present. The basal foramen large, more than one-third the length of the aedeagus. The tegmen Y-shaped; its strut more than twice as long as the lateral forks; its anterior tip bent downward. Spiculum V-shaped with curved lateral pieces; the right fork slightly longer than the left. The internal sac with a broad chitinous plate in the posterior two-thirds of the orifice floor; the latter plate with a dorsal extension on each side at the middle of the orifice; the extensions curving toward the median line above. A pair of broad chitinous plates present on each side at the closed end of the sac, between which a curved stout flagellum extends.

Phyllobrotica decorata (Say) (Pl. 13, Figs. 62a, b, c)

Aedeagus small with comparatively little curvature; flattened dorsoventrally for two-thirds of its length at the posterior and widest just anterior to the orifice. The side margins of the apex curving toward the median line to form a narrow truncated point at the posterior. The anterior third of the aedeagus

with the greatest depth; convex above and with the comparatively small foramen below; the anterior margin of the latter cleft in the median line. Tegmen Y-shaped, small, and with the strut longer than the forks. The spiculum also small and Y-shaped with one lateral element longer than the other. The internal sac longer than the aedeagus; its walls anterior to the foramen densely studded with tubercles. The flagellum was not observed.

Luperodes meraca (Say) (Pl. 13, Figs. 63a, b, c)

Aedeagus small and rather slender; asymmetrical as to sides and apex; the latter ending in a broad rounded tip. The orifice elongated and widest at its mid-region; its lateral walls low at the posterior and gradually rising to its anterior extremity, approximately one-fourth from the base of the aedeagus. Basal foramen small, narrow and ventral in position; its side and anterior margins rolled, similar to those in *Trirhabda canadensis* and *Erynephala puncticollis*. The tegmen and spiculum both Y-shaped and delicate; the latter asymmetrical and with a short anterior part. The internal sac extending almost to the posterior borders of the foramen; its inner surface armed with large hooked spines on the sides and with smaller ones above and below.

Exosoma brevicorne Jacoby (Pl. 13, Figs. 64a, b, c)

Aedeagus with comparatively little curve below; deepest and broadest in its mid-section; its posterior portion tapering, constricted at the posterior of the orifice and ending in a small point. The orifice large, extending to the mid-region of the aedeagus; its floor with a narrow groove extending almost to the posterior tip. The basal foramen comparatively large with a shape and lightly rolled borders somewhat similar to the preceding species. Tegmen Y-shaped, similar in position and form to that in *Luperodes meraca*. The spiculum crudely V-shaped with a transverse junction of the lateral elements at the anterior. The internal sac with a pair of heavy curved plates near the closed end and with several rows of long pointed spines on its inner surface near the orifice.

Cerotoma trifurcata (Forster) (Pl. 14, Figs. 65a, b, c)

Aedeagus with considerable arch from below; the portion from the foramen to the posterior tip long and narrow with its sides almost parallel but slightly wider at the orifice; the anterior portion shorter, broader and convex above; a slight transverse depression on the dorsal surface at the junction of the two portions. The side walls of the orifice low, undulated above, and sloping from the anterior to the posterior border of the aedeagus; the latter generally rounded but with a small, rather sharp point in the median line. The orifice long but less than one-half the length of the aedeagus. A short triangular shaped apical hood, its apex directed posteriorly, present above the orifice. The basal foramen large and broad. Tegmen Y-shaped with short lateral forks and an elongated, flattened strut; the latter curved ventrally at the anterior end. The spiculum V-shaped, rather delicate; somewhat asymmetrical. The internal sac extending anteriorly to the foramen; a pair of lateral plates at the

sides of the orifice, vertically placed and each with an angular projection toward the median line at its mid-section; a pair of curved lateral plates at the closed end of the sac; a group of hooked spines at each side of the flagellum when retracted. The flagellum short, of small diameter, and with a tip broadly curved to the left; the latter portion distinctly serrated on the longer side.

Andrector ruficornis (Olivier) (Pl. 14, Figs. 66a, b, c)

Aedeagus larger but very similar to that of *Cerotoma trifurcata*. The anterior portion more expanded laterally. The posterior portion longer and slightly broader; its lateral walls more parallel throughout their length, their upper edges less elevated. The posterior tip similar to that of the preceding species. The apical hood roughly triangular, its lateral sides more curved. The tegmen and spiculum similar to those in the last species but slightly larger and heavier. The vertical plates at the sides of the orifice with their medial extensions farther anterior; a pair of elongated plates, fused at the anterior, in the closed end of the sac; a group of hooked spines at each side of the mid-section. The flagellum short but of small diameter; its posterior portion curved toward the right and then sharply bent toward the anterior; the latter portion serrated on its outer side.

Chalepus dorsalis Thunberg (Pl. 14, Figs. 67a, b, c)

Aedeagus with considerable arch from below; the anterior portion, above the foramen, approximately one-half the length of the posterior; a slight dorsal constriction at the juncture of the two portions. The sides of the apical portion nearly parallel; their upper borders continuing posteriorly at approximately the same height until one-fourth from the posterior; the latter in this region curving ventrad and forming a rounded point in the median line. A triangular apical hood present above the orifice. The posterior border of the foramen projecting below the level of the curved ventral margins of the basal portion. Tegmen Y-shaped with a keeled strut. The spiculum V-shaped, one fork longer than the other. Internal sac membranous throughout, not extending anteriorly to the foramen. A stout flagellum present.

Baliosus ruber (Weber) (Pl. 14, Figs. 68a, b, c)

Aedeagus approximately the same length and of the same form as in *Chalepus dorsalis*. The anterior portion forming less of the total length; its side walls of less depth and with greater upward curve of their ventral margins. The side walls of the apical portion not so high as in the preceding form but forming a greater angle with the ventral wall at the posterior. The posterior tip of the aedeagus rounded, not pointed. A broad apical hood above the orifice, with a straight posterior margin and with lateral plates extending inward on the sac. The tegmen and spiculum similar to those in *Chalepus dorsalis*; the spiculum smaller and more U-shaped. A stout, curved flagellum extending into the membranous sac at its closed end.

Microhophala vittata (Fabricius) (Pl. 14, Figs. 69a, b, c)

Aedeagus approximately the same size and similar to that in *Baliosus ruber*; its anterior portion forming less of the total length; its posterior portion with greater upward arch, its side walls curved more toward the median line above, and with its ventral surface more regularly curved. The posterior border of the aedeagus rounded at the sides and with a point in the median line; the latter point with a slight upward curve. The apical hood broad but with a curved posterior border. Tegmen Y-shaped; its strut keeled. The spiculum U-shaped and delicate. The internal sac membranous, not extending to the foramen. A stout flagellum present.

Physonota unipunctata var. *quinquepunctata* Walsh (Pl. 15, Figs. 70a, b, c)

Aedeagus very large and considerably arched; the anterior portion broad, convex above, but forming less of the length than remainder of the aedeagus. The apical portion constricted from the sides at its mid-section and of greatest depth and width at the middle of the orifice. The sides of the apex curving toward the mid-line and then posteriorly to form a small squared tip; the latter bent slightly upward. The basal foramen large; its posterior border formed by a prominent ventral extension of the lower wall of the aedeagus. The tegmen, forming a crude Y; its strut a thin sheet slightly elevated in the median line, and with its lateral margins directed downward. The spiculum small, forming a wide V. The internal sac, short, slightly more than half the length of the apical portion; a pair of dorso-lateral plates at the orifice; a pair of elongated ejaculatory guides near the ventral wall of the closed end; above the latter a single plate with broad anterior and slender posterior halves. The flagellum short and with a diameter slightly greater than the ejaculatory duct which joins it at the anterior extremity.

Deloyala (= *Chirida* auth.) *guttata* (Olivier) (Pl. 15, Figs. 71a, b)

Aedeagus of the same general form as the preceding one. The sides of the posterior portion more nearly parallel, slightly more separated at the posterior end of the orifice. The apex curved at the sides but ending in a broad squared tip. A pair of dorso-lateral plates at the orifice on the dorsal fold of the internal sac. The basal foramen large; its posterior margin prominently extending ventrad. Tegmen similar in form to that of the preceding species. No spiculum found. The internal sac short, barely extending two-thirds of the distance to the foramen; its closed end containing a pair of broad plates, vertically placed, and posterior to the latter a pair of slender, contiguous or fused plates (ejg) in the median line. A short flagellum, with a diameter approximately twice that of the ejaculatory duct, extends between and under the pairs of plates at the closed end of the sac.

Plagiometriona (= *Deloyala* auth.) *clavata* (Fabricius) (Pl. 15, Figs. 72a, b)

Aedeagus longer than in *Deloyala guttata*, considerably constricted above the ventrally projecting posterior border of the foramen. The posterior portion with less depth but slightly greater width than in the preceding species; the

general form of the apex very similar but of greater length in the median line posterior to the orifice. Tegmen similar to those in the last two species described. The plates in the dorsal fold of the sac at the orifice broader at their posterior ends, their inner borders curving more abruptly away from median line. Pairs of plates, similar to those in *Deloyala guttata* but slightly different in size and arrangement, present at the closed end of the sac. The flagellum short, of greater diameter than the ejaculatory duct, and with a slight upward curve toward its pointed tip.

Discussion

The general opinion of many authors, including those previously listed and others, is that the genital structures were originally derived from paired appendages although not all are agreed as to the exact portions of the appendages so utilized. Metcalfe in her study of *Gastrophysa* (= *Gastroidea* auth.) *polygona*, one of the Chrysomelidae, has shown that the embryology of this species supports the above opinion. Singh-Pruthi has found the same to be true in the development of *Tenebrio*. The genitalia then which most nearly show a double character would seem to approximate most closely the ancestral form.

Of all the genitalia used in the present study, those of *Orsodacne atra* var. *childreni* because of the two-pointed apex, the very deeply cleft basal portion, and the bilobed tegmental cap indicate most strikingly such a double origin. The writer, therefore, considers this species to be the most primitive. Sharp and Muir, although believing that the aedeagus has a single origin, have also concluded that the genitalia of a different species of *Orsodacne* have the most primitive form of any shown by the Chrysomelidae as now constituted. The presence of a tegmen with a tegmental cap and a poorly specialized internal sac is the basis for their opinion. The writer agrees with Sharp and Muir that the latter structures are indicative of a primitive form but also considers that the evidence presented by other authors concerning the double origin of the aedeagus is well supported in this species.

General similarity in the forms of the aedeagus and of the tegmen has been upheld as indicative of common origin in this investigation. The spiculum gastrale shows a greater tendency toward variation, is apparently absent in some species and is, therefore, not so useful. The use of the aedeagus and tegmen follows, in general, the method of Sharp and Muir. These authors especially have emphasized the importance of the tegmental cap as indicative of a lower form.

The authors just mentioned imply that perhaps *Orsodacne* should be removed from the family as it is now constituted and should be placed below the Bruchidae which they believe bears some relationship to the Chrysomelidae. They also state from the study of *Timarcha geniculata* that this form having the same general type of tegmen and basal portion should perhaps hold a position nearer *Orsodacne* than others of the present family Chrysomelidae. The writer considers that the genitalia of *Timarcha intricata*, closely resembling those of the species used by Sharp and Muir, give support to this

statement of these authors. The only other species of the seventy-two studied by the author which have the tegmental cap are *Donacia piscatrix* and *Macrolea nigricornis*. It is true that the basal portion of the aedeagus in these two is not cleft and that the tegmental cap is of different shape but its presence in both would seem to place them nearer *Timarcha* than others of this family.

The author is of the opinion that until the genitalia of more species of the subfamily Criocerinae are studied, as well as of many other species of the family, little can be learned of their relationships. Only two species, *Crioceris asparagi* and *Lema trilineata* (Pl. 1, Figs. 4 and 5 respectively), were available to the author.

Representatives of the genera, *Megalostomis*, *Babia*, *Urodera* and *Saxinis* (Pl. 2, Figs. 7-10), all of the subfamily Clytrinae, show considerable conformity as to aedeagus, tegmen and spiculum and are apparently rightly placed in the same group. The presence of long hairs at or near the orifice and the similarity of the complex armature of the sac give further evidence of their relationship. *Antipus laticlavus* (Pl. 1, Fig. 6) also included, at present, in this subfamily shows less similarity in general form of the aedeagus; the specialization of the sac armature, its tegmen and spiculum, however, agree quite well in general plan. Of the species of this subfamily studied, *Babia quadriguttata* shows the most specialization of the sac at the orifice.

The subfamily Cryptocephalinae is here represented by one species from each of the following genera: *Griburius*, *Pachybrachis*, *Monachulus*, *Cryptocephalus* (Pl. 3, Figs. 12-15). In general these species are similar as to all three parts of the genitalia with *Pachybrachis* and *Monachulus* apparently more closely related than *Griburius* and *Pachybrachis* which now are included in the same tribe. *Cryptocephalus* with its peculiar apical hood and the most complex armature of the sac at the orifice presents the most specialization. The general forms of the aedeagus, tegmen and spiculum of the species studied from this subfamily are similar to those of the subfamily Clytrinae. Long hairs on the apical portion may also be taken as further evidence of the relationship of these two subfamilies. Since the last mentioned structures were found only on the aedeagi in three subfamilies, their presence on the lower surface of the apex in *Exema conspersa* var. *dispar* (Pl. 2, Fig. 11) may indicate that the subfamily Chlamydinae should occupy a place near the last two discussed. The form of the aedeagus of this species is considerably different and more investigation is needed to establish relationship.

Twelve species of the subfamily Eumolpinae were studied. While there is a general similarity in the character of the aedeagus, as well as in the tegmen, there were certain interesting differences noted which probably indicate two smaller groups of related genera within this subfamily. One group composed of the genera *Chrysodina* (Pl. 3, Fig. 16), *Colaspis* (Pl. 3, Fig. 17), *Glyptoscelsis* (Pl. 5, Fig. 23), and *Chrysochus* (Pl. 5, Figs. 26, 27) have an aedeagus with a distinct transverse depression on the dorsal surface of the posterior region of the basal portion; the ventral surface at the posterior border of the foramen is projected prominently in a postero-ventral direction at the sides,

forming vertical grooves; the strut of the tegmen has a single point at the anterior. The genera *Xanthonia* (Pl. 4, Fig. 19), *Metachroma* (Pl. 4, Fig. 21), *Colaspidea* (Pl. 5, Fig. 24), and *Typophorus* (Pl. 5, Fig. 25) constitute the second group indicated. They possess aedeagi which lack the depression on the dorsal surface of the basal portion; the posterior borders of their foramina are roundly curved and do not have the vertical grooves at the sides; the anterior end of the tegmen is broad and bilobed, giving the whole of the tegmen an H-shape. *Fidia viticida* (Pl. 4, Fig. 20) possesses an aedeagus characteristic of the second group but its tegmen resembles those of the first. The spicula in this group vary considerably in size, those of the genus *Chrysochus* being very small; in *Xanthonia*, *Metachroma*, *Adoxus* and *Colaspidea* there appears to be a smaller secondary spiculum present. A double pointed apex, or what apparently is a modified form of such, is seen in *Xanthonia*, *Fidia*, *Metachroma* and *Adoxus*. The aedeagi of *Chrysochus auratus* and *C. cobaltinus* (Pl. 5, Figs. 26, 27) show marked similarity of form, a fact which is also true of the external form of the beetles.

Thirty-one species of the subfamily Chrysomelinae, as it is now constituted, have been studied. With the possible exceptions of *Timarcha* and a few genera which will later be mentioned, there is considerable similarity exhibited in the general character of aedeagus, tegmen and spiculum. The general simplicity of the internal sac in the greater portion of the group approximates that of *Timarcha*. However, in the genera, *Plagiodera* (Pl. 11, Fig. 53), *Gastrophysa* (Pl. 11, 12, Figs. 54-56), and *Chrysomela* (Pl. 12, Figs. 57, 58), a greater specialization of this part is found. In addition to this, differences in aedeagus and tegmen are also seen. The general forms of all three parts of the genitalia show considerable correspondence in the following genera: *Labidomera*, *Leptinotarsa*, *Zygogramma*, *Calligrapha*, and *Chrysolina*. Those of *Entomoscelis* and *Prasocuris* (Pl. 6, Figs. 29, 30) show general similarity but possess an internal sac of slightly greater specialization. Their correspondence is probably sufficient to justify placing them near the group of five genera mentioned above.

Leptinotarsa and *Chrysolina* show a closer relationship to each other than to the other genera mentioned. This is indicated by the size and general shape of the aedeagus and by the general conformity of tegmen and spiculum. *Leptinotarsa lineolata* (Pl. 7, Fig. 34) shows the greatest difference in size and shape of the apical portion of the aedeagus. *Chrysolina flavomarginata* (Pl. 10, Fig. 50) because of its tapering apex probably represents a "connecting link" between the two genera. The presence of lateral points on the apex of the other two species of *Chrysolina* apparently indicates a relationship to a *Zygogramma*-*Calligrapha* group.

The species of this latter group, with the exception of *Calligrapha praeclisis* (Pl. 9, Fig. 42), show considerable correspondence of genital structures. This one exception, because of the shape of the aedeagus, the spiculum, and the shape and curvature of the flagellum, evidently bears closer relationship to *Labidomera clivicollis* (Pl. 6, Fig. 31) than to the other species of the genus *Calligrapha*. The genital parts of the remainder of the *Zygogramma*-*Calligrapha*

group show, in general, only minor differences in the shape of the posterior tip of the aedeagus and the tip of the flagellum. *Calligrapha similis* (Pl. 8, Fig. 41) and *C. elegans* (Pl. 9, Fig. 43), by the presence of a median extension of the apex of the aedeagus and a peculiar structure of the tip of the flagellum, show the greatest variation of the group and a close relationship to each other. Likewise, closer correspondence of these same parts indicates the same thing with respect to *C. lunata* (Pl. 8, Fig. 40) and *C. multipunctata* (Pl. 10, Fig. 46) in one case and in another between *C. spireae* (Pl. 9, Fig. 45) and *C. bigsbyana* (Pl. 10, Fig. 47). The latter indication is interesting to note since *C. bigsbyana* was at one time considered a variety of *C. multipunctata*.

*Plagioder*a and *Gastrophysa* show similar aedeagi, apical hoods and chitinizations of the internal sac. *Chrysomela* (Pl. 12, Figs. 57, 58) presents some similarity of the shape of the aedeagus, tegmen, and spiculum to the last two genera.

The species of the subfamily Galerucinae possess a heterogeneous assortment of genitalia. From those studied three possible groups are suggested. The first group, composed of *Trirhabda* (Pl. 12, Fig. 59) and *Erynephala* (Pl. 13, Fig. 60) have the aedeagus with a short abrupt curve at the anterior, above a small almost terminal foramen; the internal sac is without tubercles or spines on its inner surface. *Phyllobrotica*, *Luperodes*, and *Exosoma* (Pl. 13, Figs. 62-64) of the second group agree in the general position of the foramen and in having tubercles or spines on the inner surface of the sac. The third group is composed of *Cerotoma* and *Andrector* (Pl. 14, Figs. 65, 66). Their genital parts are so similar that very close relationship is plainly indicated. On the basis of this similarity the author questions the importance of their separation into two genera. The first and second groupings suggested are apparently rightly placed in the same subfamily. The third group, however, shows little correlation with them. The general plan of the aedeagus indicates a much closer relationship to the subfamily Eumolpinae. The genitalia of *Diabrotica* (Pl. 13, Fig. 61) gives indication that this genus should be placed near the *Cerotoma-Andrector* group. Since there is so much variation of the genitalia of this subfamily and since comparatively few of the genitalia are here studied much further work is deemed necessary before definite conclusions can be drawn concerning them.

Chalepus, *Baliosus*, and *Microrhopala* (Pl. 14, Figs. 67-69) of the subfamily Hispinae show such similarity in the form of genital parts, that had they been studied before the external anatomy of the beetles, they would undoubtedly have been placed in the same genus. The same could well be stated for *Physonota*, *Deloyala*, and *Plagiometriona* (Pl. 15, Figs. 70-72) of the subfamily Cassidinae. While the genitalia of these two subfamilies show minor peculiarities of their own, their general form is strikingly similar to those obtained from the Eumolpinae. It is the opinion of the author that further investigations will definitely reveal relationships to this group.

The conclusions drawn have been based only upon comparisons of the genitalia. Further study of the adult genitalia of many other species and also

of the embryological development of these structures will be necessary before more definite statements concerning the phylogenetic relationships within this large family of beetles can be made.

Summary

1. This study supports the evidence of Sharp and Muir (1912) that *Orsodacne* is probably the most primitive of all the Chrysomelidae. However, in contradiction to Muir (1918), the writer believes that the aedeagi of the species within this genus support the statements of other authors that these structures in insects have a double origin.

2. The genitalia of *Timarcha intricata* show close similarity to those of *T. geniculata* which were studied by Sharp and Muir and add support to the statement of these authors that the genus *Timarcha* should be placed near *Orsodacne* in a phylogenetic arrangement of genera.

3. *Donacia* and *Macrolea*, because of the tegmental cap and the simplicity of the internal sac, should follow *Timarcha* in such an arrangement.

4. Evidence of a rather close relationship is indicated by the genitalia of the subfamilies Clytrinae and Cryptocephalinae. The Chlamydinae, when further study is made, will perhaps show a relationship not far removed from the last mentioned subfamilies.

5. The Eumolpinae show considerable conformity as to genital parts but two minor divisions of this subfamily seem to be indicated by certain characteristics of the aedeagus and tegmen: (1) *Chrysodina-Colaspis-Glyptoscelis-Chrysochus* and (2) *Xanthonia-Metachroma-Colaspidea-Typophorus*.

6. The genitalia of the Chrysomelinae, with the exception of *Timarcha*, show fair correspondence of parts. Three groups of related genera are indicated: *Leptinotarsa-Chrysolina*, *Zygogramma-Calligrapha*, and *Plagioder-Gastrophysa*. The genus *Chrysomela* may later be shown to bear relationship to the last. Interesting close relationships in this subfamily not evident in the external structure, are indicated by the genitalia.

7. The genitalia of Galerucinae which were studied suggest three groups of related genera: (1) *Trirhabda-Erynephala*, (2) *Phyllobrotica-Luperodes-Exosoma*, and (3) *Cerotoma-Andrector*. The first and second of these show sufficient similarity of genital parts to be included in the same subfamily. The third appears to be much more closely related to the Eumolpinae.

8. The Hispinae are shown to be a very closely related group. General similarity of the genital structures to those of the Eumolpinae is shown, probably indicating relationship between these subfamilies.

9. The genitalia of the Cassidinae give indication of close relationship. Their similarity to those of the Eumolpinae is likewise seen and probable relationship is indicated.

10. The evidence presented in this investigation supports Sharp and Muir in their statement that such investigations are of value and will eventually lead to a better knowledge of the true relationships existing within the Coleoptera.

REFERENCES

- BARBER, H. S. AND J. C. BRIDWELL. 1940—Dejean Catalogue Names (Coleoptera). Bull. Brooklyn Ent. Soc. **35**(1):1-12.
- BLAKE, DORIS H. 1927—A Revision of the Beetles of the Genus *Oedionychus* occurring in America, North of Mexico. Proc. U. S. Nat. Mus. **70**(23):1-44.
- 1932—Revision of the Species of Beetles of the Genus *Trirhabda*, North of Mexico. Proc. U. S. Nat. Mus. **79**(2):1-36.
- CHRISTOPHERS, S. R. 1922—The Development and Structure of the Abdominal Segments and Hypopygium in the Male Mosquito with Observations on the Terminal Segments of the Larva. Ind. Jour. Med. Res. **10**:530-572.
- AND F. W. CRAGG. 1921-1922—On the so-called Penis of the Bed-bug (*Cimex lenticularis* L.) and on the Homologies generally of the Female and Male Genitalia of this Insect. Ind. Jour. Med. Res. **9**:445-464.
- DELONG, DWIGHT M. 1931—A Revision of the American Species of *Empoasca* known to occur north of Mexico. U. S. Dept. Agric., Tech. Bull. No. **231**:1-60.
- GEORGE, C. J. 1928—The Morphology and Development of the Genitalian and Genital Ducts of Homoptera and Zygoptera as shown in the Life Histories of *Philaenus* and *Agriion*. Quar. Jour. Micr. Sci. **72**:447-486.
- HAVILAND, MAUD D. 1921—Bionomics and Development of *Lygoceros cameroni*, Kiefer (Procto trypoidea-Cerophronidae), Parasites of *Aphidius* (Braconidae). Quar. Jour. Micr. Sci. **65**(258 N.S.):101-127.
- KRAEPELIN, C. 1873—Untersuchungen über den Bau, Mechanismus und Entwicklungsgeschichte des Stachels der bienenartigen Thiere. Zeit. f. wiss. Zool. **23**:289-330.
- KULAGIN, N. 1897-1898—Beiträge zur Kenntnis der Entwicklungsgeschichte von *Platygaster*. Zeit. f. wiss. Zool. **63**:195-235.
- LENG, CHARLES W. 1920—Catalogue of the Coleoptera of America, North of Mexico. John D. Sherman, Jr., Mount Vernon, N. Y.
- METCALF, C. L. 1921—The Genitalia of the Male Syrphidae: Their Morphology with Especial Reference to its Taxonomic Significance. Ann Ent. Soc. Amer. **14**(3):169-226.
- METCALFE, MARGOT E. 1932—The Structure and Development of the Reproductive System in the Coleoptera with Notes on its Homologies. Quar. Jour. Micr. Sci. **75**:49-130.
- MICHAELIS, G. 1900—Bau und Entwicklung des männlichen Begattungsapparates der Honigbiene. Zeit. f. wiss. Zool. **67**:439-460.
- MUIR, F. 1918—Notes on the Ontogeny and Morphology of the Male Genital Tube in Coleoptera. Trans. Ent. Soc. London **1918**:223-229.
- NEWELL, ANNA G. 1918—The Comparative Morphology of the Genitalia of Insects. Ann. Ent. Soc. Amer. **11**(2):109-156.

- SHARP, D. AND F. MUIR. 1912—The Comparative Anatomy of the Male Genital Tube in Coleoptera. Trans. Ent. Soc. London 1912:477-642.
- SINGH-PRUTHI, HEM. 1924—On the post embryonic Development and Homologies of the Male Genital Organs in *Tenebrio molitor* L. (Coleoptera). Proc. Zool. Soc. London 3:857-868.
- 1925—The Development of the Male Genitalia in the Homoptera with preliminary Remarks on the Nature of these Organs in other Insects. Quar. Jour. Micr. Sci. 69:59-96.
- VERSION, E. AND E. BISSON. 1896—Die postembryonale Entwicklung der Ausführungsgänge und der Nebendrüsen beim männlichen Geschlechtsapparat von *Bombyx mori*. Zeit. f. wiss. Zool. 61:318-337.
- ZANDER, E. 1900—Beiträge zur Morphologie der männlichen Geschlechtsanhänge der Hymenopteren. Zeit. f. wiss. Zool. 67:461-489.
- 1901—Beiträge zur Morphologie der männlichen Geschlechtsanhänge der Trichopteren. Zeit. f. wiss. Zool. 70:192-235.
- 1903—Beiträge zur Morphologie der männlichen Geschlechtsanhänge der Lepidopteren. Zeit. f. wiss. Zool. 74:557-615.

EXPLANATION OF PLATES

The drawings of the genitalia have been made as simple as possible to aid in their interpretation by the reader. Those pertaining to the same species have been given the same number with the addition of letters, a, b, c, d, to distinguish the different views and parts: a, lateral, or slightly dorsolateral, view of aedeagus and tegmen; b, dorsal, or dorsocaudal, view of aedeagus; c, spiculum gastrale, usually dorsal, or dorsocaudal, view; d, secondary spiculum gastrale. The scale of 0.05 mm. has been projected to give indication of the size relation of the structures. The spiculum gastrale, where shown, has the same magnification as the lateral view of aedeagus and tegmen, and only one scale is used for these drawings.

LIST OF ABBREVIATIONS

ao.....	apical orifice (orifice)	ejd.....	ejaculatory duct
aph.....	apical hood	ejg.....	ejaculatory guide
bf.....	basal foramen (foramen)	fg.....	flagellum
dp.....	median dorsal plate	ins.....	internal sac (sac)
	(dorso-lateral plate when median	lp.....	lateral plate
	dorsal plate absent)	tg.....	tegmen
		tgc.....	tegmental cap

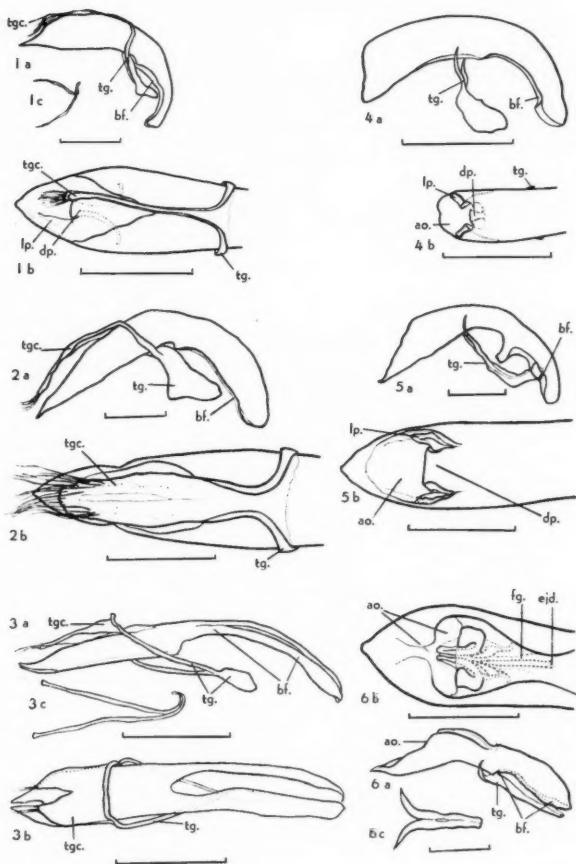


PLATE 1: Figs. 1a-1c. *Macrolea* (= *Haemonia* auth.) *nigricornis* (Kby.). Figs. 2a, 2b. *Donacia piscatrix* Lac. Figs. 3a-3c. *Orsodacne atra* var. *childreni* Kby. Figs. 4a, 4b. *Crioceris asparagi* (L.). Figs. 5a, 5b. *Lema trilineata* (Oliv.). Figs. 6a-6c. *Antipus laticlavus* (Forst.)

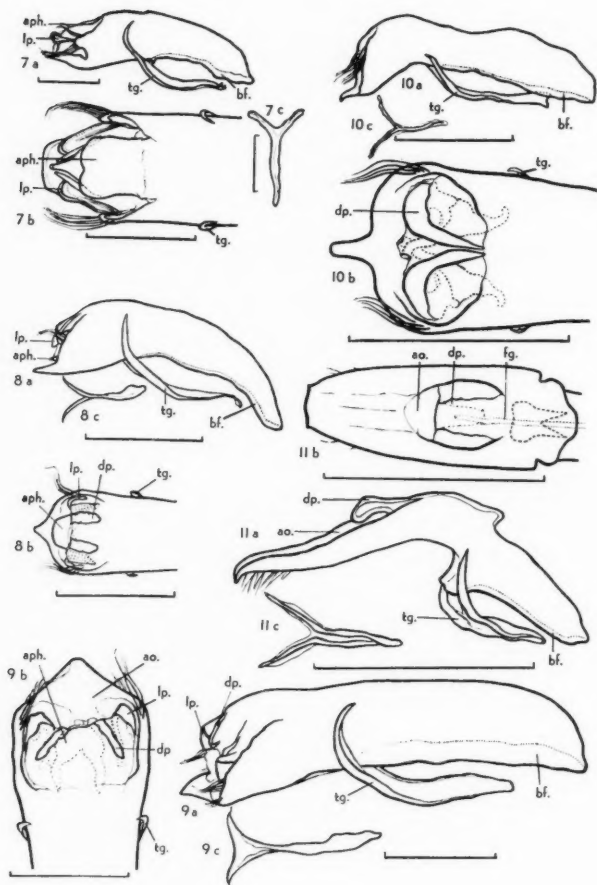


PLATE 2: Figs. 7a-7c. *Megalostomis subfasciata* (Lec.). Figs. 8a-8c. *Babia quadriguttata* (Oliv.). Figs. 9a-9c. *Urodera crucifera* Lac. Figs. 10a-10c. *Saxinis omogera* Lac. Figs. 11a-11c. *Exema conspersa* var. *dispar* Lac.

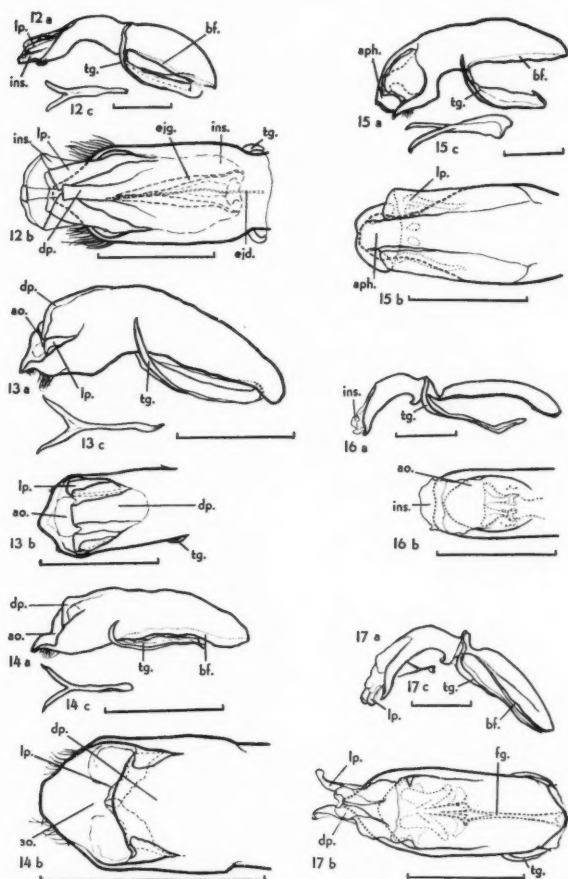


PLATE 3: Figs. 12a-12c. *Griburius equestris* (Oliv.). Figs. 13a-13c. *Pachybrachis luridus* (Fab.) Figs. 14a-14c. *Monachulus saponatus* (Fab.). Figs. 15a-15c. *Cryptocephalus leucomalis* Suffr. Figs. 16a, 16b. *Chrysodina globosa* (Oliv.). Figs. 17a-17c. *Colaspis brunnea* (Fab.).

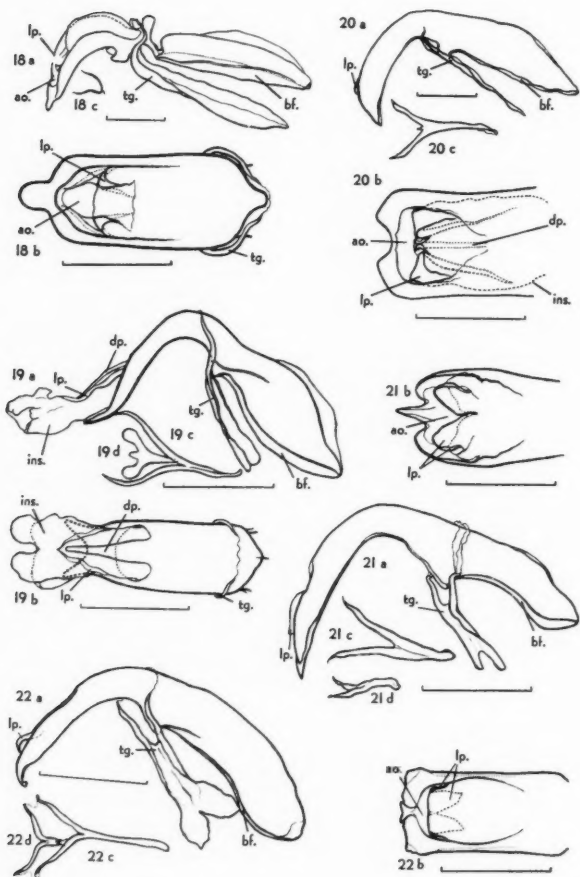


PLATE 4: Figs. 18a-18c. *Rhabdopterus picipes* (Oliv.) Figs. 19a-19d. *Xanthonia villosula* (Melsh.). Figs. 20a-20c. *Fidia viticida* Walsh. Figs. 21a-21d. *Metachroma parallelum* Horn. Figs. 22a-22d. *Adoxus obscurus* (L.).

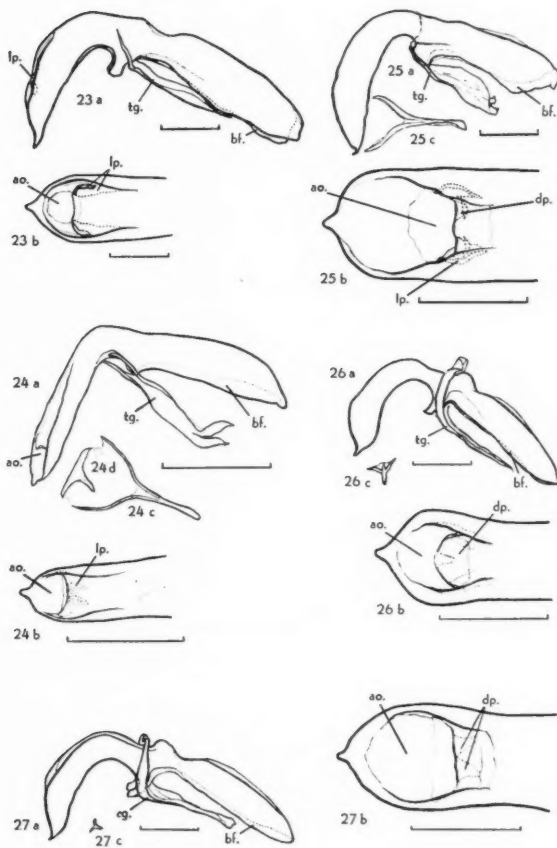


PLATE 5: Figs. 23a, 23b. *Glyptoscels pubescens* (Fab.). Figs. 24a-24d. *Colaspidea varicolor* Cr. Figs. 25a-25c. *Typophorus viridicyaneus* (Cr.). Figs. 26a-26c. *Chrysochus auratus* (Fab.). Figs. 27a-27c. *Chrysochus cobaltinus* Lec.

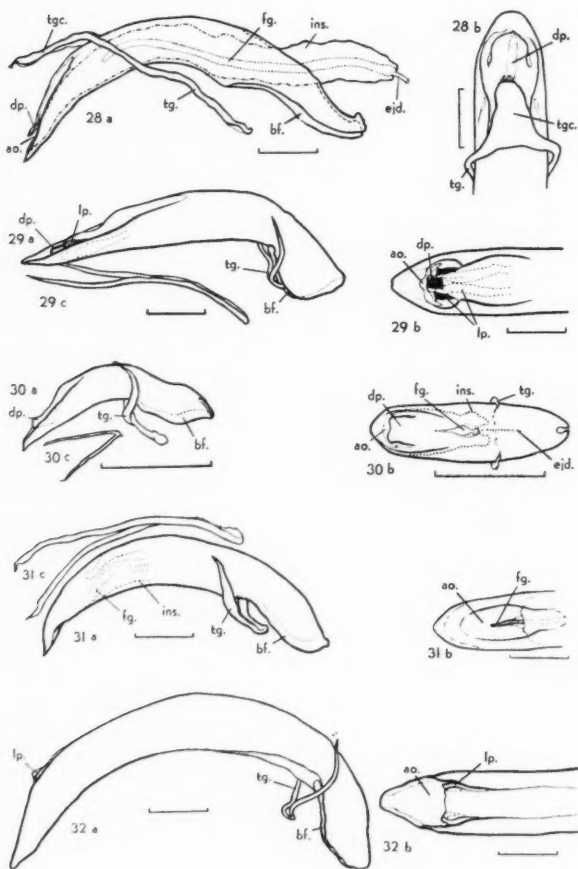


PLATE 6: Figs. 28a, 28b. *Timarcha intricata* Hald. Figs. 29a-29c. *Entomoscelis adonidis* (Pallas). Figs. 30a-30c. *Prasocuris vittata* (Oliv.). Figs. 31a-31c. *Labidomera clivicollis* (Kby.). Figs. 32a, 32b. *Leptinotarsa rubiginosa* (Rogers).

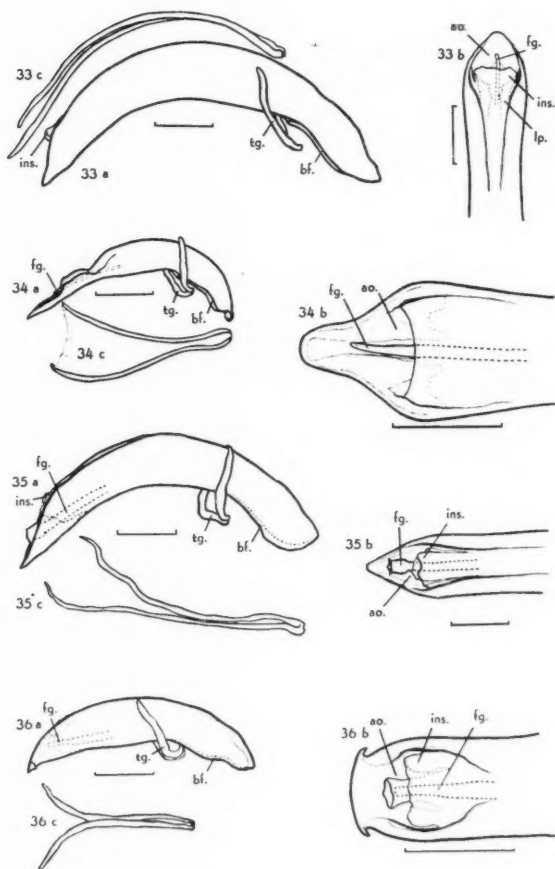


PLATE 7: Figs. 33a-33c. *Leptinotarsa haldemani* (Rogers). Figs. 34a-34c. *Leptinotarsa lineolata* Stål. Figs. 35a-35c. *Leptinotarsa decemlineata* (Say). Figs. 36a-36c. *Zygotogramma exclamatoris* (Fab.).

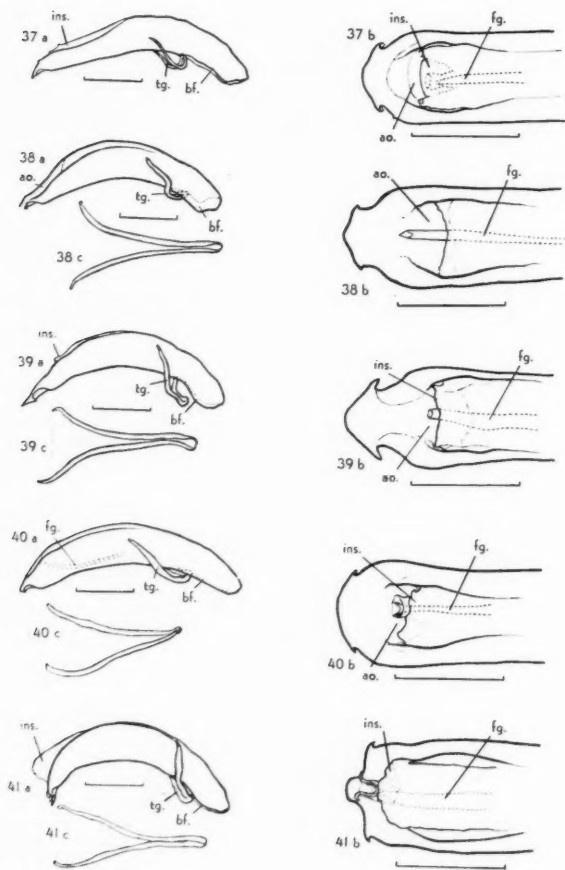


PLATE 8: Figs. 37a, 37b. *Zygogramma continua* Lec. Figs. 38a-38c. *Zygogramma suturalis* var. *casta* Rogers. Figs. 39a-39c. *Zygogramma disrupta* Rogers. Figs. 40a-40c. *Calligrapha lunata* var. *hybrida* (Say). Figs. 41a-41c. *Calligrapha similis* Rogers.

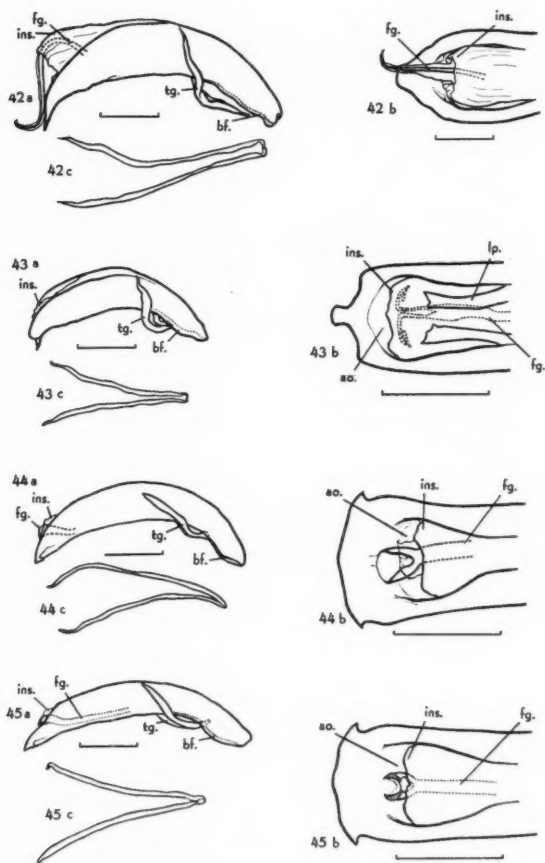


PLATE 9: Figs. 42a-42c. *Calligrapha praecelsis* Rogers. Figs. 43a-43c. *Calligrapha elegans* (Oliv.). Figs. 44a-44c. *Calligrapha scalaris* Lec. Figs. 45a-45c. *Calligrapha spireae* (Say).

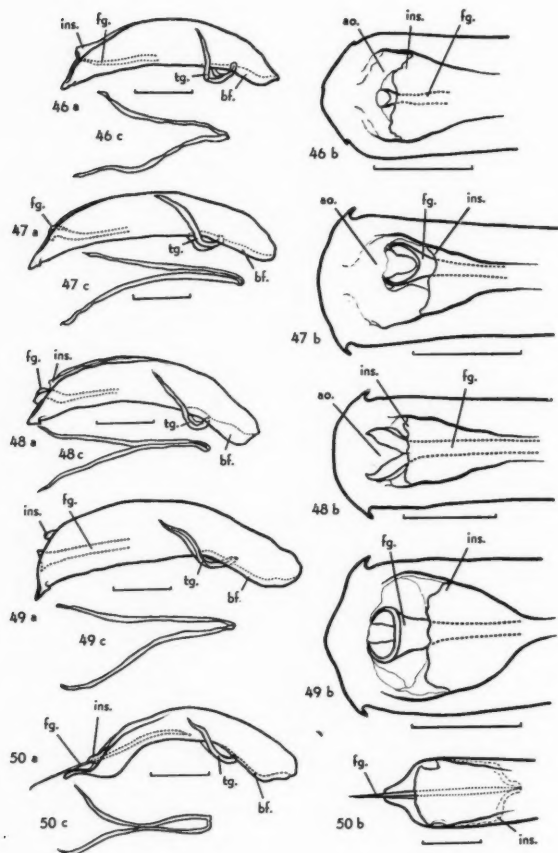


PLATE 10: Figs. 46a-46c. *Calligrapha multipunctata* (Say). Figs. 47a-47c. *Calligrapha bigsbyana* (Kby.). Figs. 48a-48c. *Calligrapha sigmoidea* Lec. Figs. 49a-49c. *Calligrapha serpentina* Rogers. Figs. 50a-50c. *Chrysolina* (= *Chrysomela* auth.) *flavo-marginata* (Say).

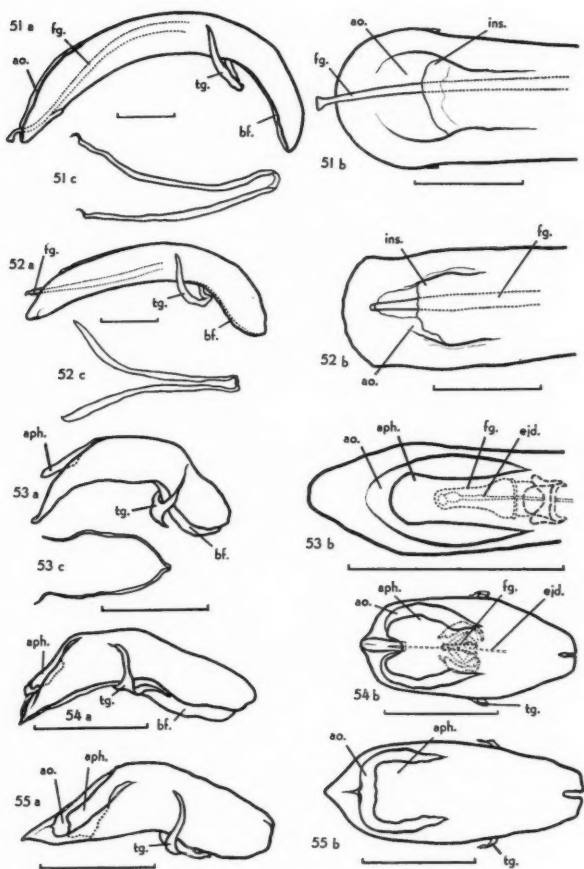


PLATE 11: Figs. 51a-51c. *Chrysolina* (= *Chrysomela* auth.) *cribraria* (Rogers). Figs. 52a-52c. *Chrysolina* (= *Chrysomela* auth.) *montevagens* (Lec.). Figs. 53a-53c. *Plagioderia versicolora* (Laich.). Figs. 54a, 54b. *Gastrophysa* (= *Gastroides* auth.) *polygoni* (L.). Figs. 55a, 55b. *Gastrophysa* (= *Gastroides* auth.) *dissimilis* (Say).

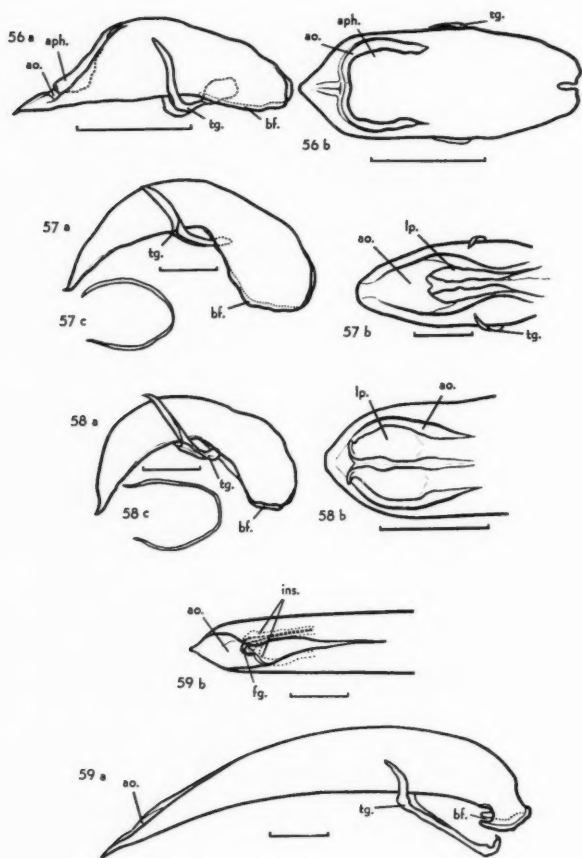


PLATE 12: Figs. 56a, 56b. *Gastrophysa* (= *Gastroidea* auth.) *cyanea* Melsh. Figs. 57a-57c. *Chrysomela* (= *Lina* auth.) *interrupta* (Fab.). Figs. 58a-58c. *Chrysomela* (= *Lina* auth.) *scripta* (Fab.). Figs. 59a, 59b. *Trirhabda canadensis* (Kby.).

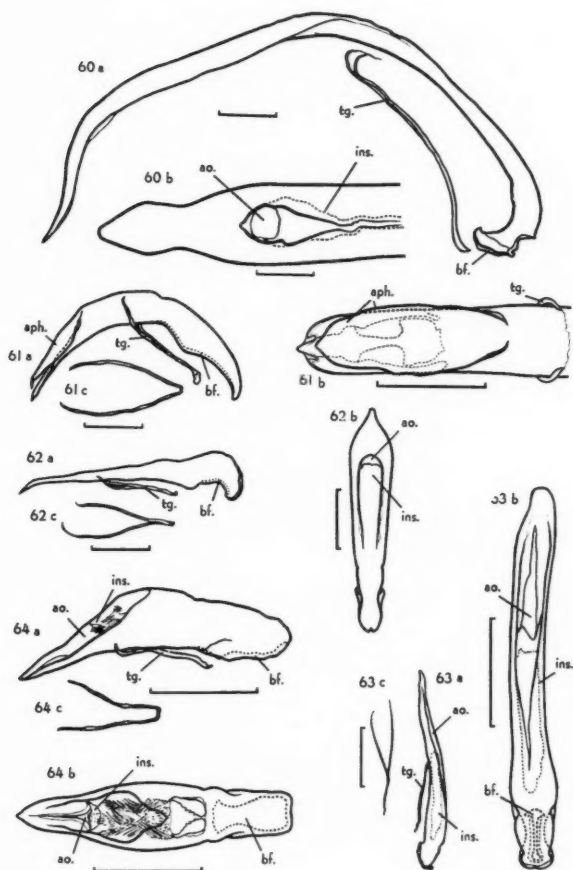


PLATE 13: Figs. 60a, 60b. *Erynephalia* (= *Monoxia* auth.) *puncticollis* (Say). Figs. 61a-61c. *Diabrotica duodecempunctata* (Fab.). Figs. 62a-62c. *Phyllobrotica decorata* (Say). Figs. 63a-63c. *Luperodes meraca* (Say). Figs. 64a-64c. *Exosoma brevicorne* Jac.

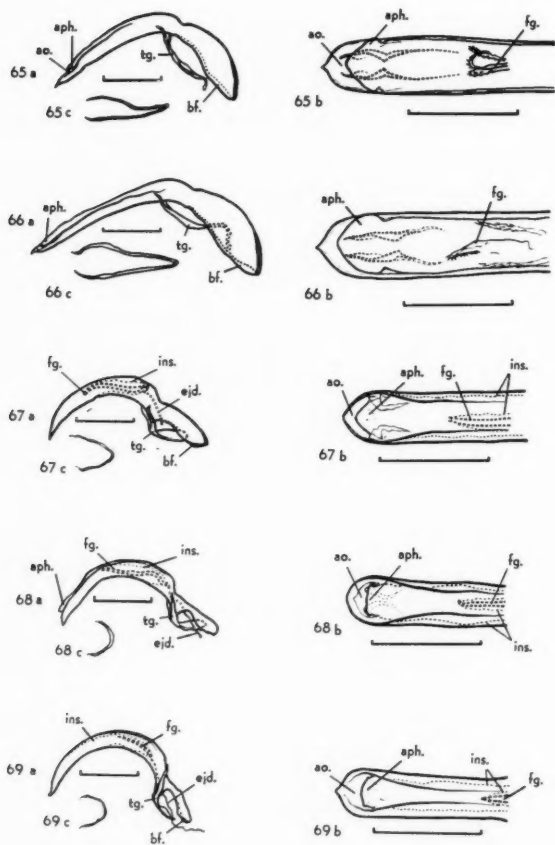


PLATE 14: Figs. 65a-65c. *Cerotoma trifurcata* (Forst.). Figs. 66a-66c. *Andrector ruficornis* (Oliv.). Figs. 67a-67c. *Chalepus dorsalis* Thunb. Figs. 68a-68c. *Baliosus ruber* (Web.). Figs. 69a-69c. *Microrhopala vittata* (Fab.).

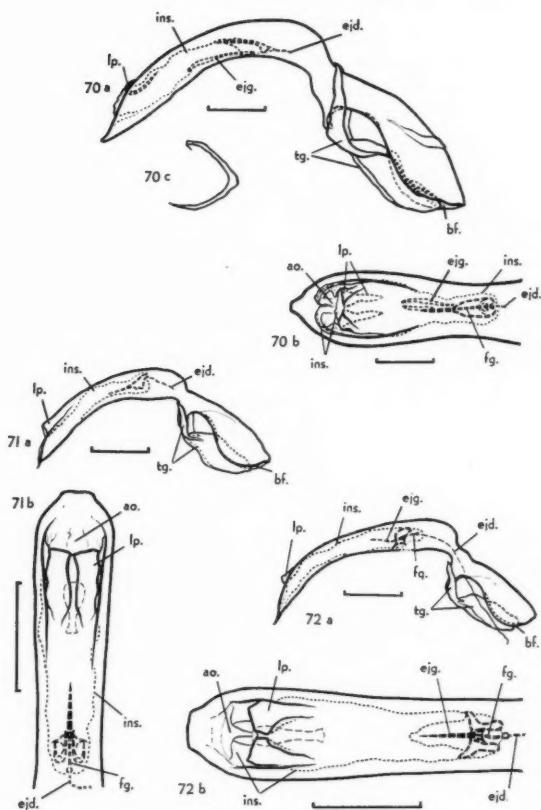


PLATE 15: Figs. 70a-70c. *Physonota unipunctata* var. *quinquepunctata* Walsh. Figs. 71a, 71b. *Deloyala* (= *Chirida* auth.) *guttata* (Oliv.). Figs. 72a, 72b. *Plagiometriona* (= *Deloyala* auth.) *clavata* (Fab.).

The Homes and Social Habits of the Wood-Mouse (*Peromyscus leucopus noveboracensis*) in Southern Michigan¹

Arnold J. Nicholson

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Introduction

Information about the life histories of the smaller mammals is generally lacking, chiefly because of the difficulty of studying these timid and mostly nocturnal animals. The artificial nest boxes here described provide a means for the investigation of certain phases of the life histories of mice and other small mammals which previously could not be directly studied. Although nest boxes have been much used in the past for the study of birds they seem not previously to have been used for mammals.

Most of the data secured in the present study pertains to the wood-mouse (*Peromyscus leucopus noveboracensis*), but some information was secured also about the habits of the prairie deer-mouse (*Peromyscus maniculatus bairdii*). The value of the nest boxes for these studies is attested by the considerable number of individual animals kept under observation, these constituting a large proportion of the total wood-mouse populations on the areas studied.

ACKNOWLEDGEMENTS

This study was carried out under the direction of Lee R. Dice, and has been in part supported by the Laboratory of Vertebrate Genetics, University

¹ A condensation of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, in the University of Michigan.

of Michigan. William H. Burt has given helpful advice during the course of the investigation. The facilities of the Edwin S. George Reserve were placed at my disposal by Frederick M. Gaige.

Methods

Throughout the course of the study, the field operations were conducted in such a manner that the conditions would be kept as nearly natural as possible, and so that the animals using the artificial nest boxes would not be disturbed more than necessary.

CONSTRUCTION OF THE NEST BOXES

The nest boxes (Fig. 1) varied in size from 4 x 4 x 3 inches to 9 x 7 x 5 inches. They were generally cuboidal in shape, and were constructed of one-half inch lumber. The animals used boxes made of new lumber just as readily as those made of old lumber. Likewise, boxes constructed of lumber soaked in linseed oil, to prevent warping, were used as readily as those not soaked in oil.

Each box has a removable top to facilitate examination. Experiments indicate that tops constructed of wood are better than those made of metal or other material, for the wood tends to reduce the amount of condensed moisture.

To facilitate the examination of the animals inside of the nest box, there is

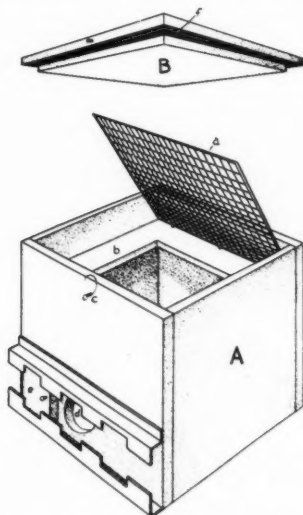


Fig. 1. Diagram of a nest box. Key: A-nest box, (a) inner door, (b) shelf for inner door, (c) hook to fasten cover, (d) opening to box, and (e) sliding door; B-cover of box, (f) sheet of tar paper.

an inside door, below the lid, made of $\frac{1}{3}$ inch mesh hardware cloth. It is therefore possible to remove the lid of the box and to determine whether any animals are present without danger of their escaping. This screen door must be fastened so that animals can not push their way above it and thereby become imprisoned above the screen. A shelf to support the inner screen door extends around the inside of the box. This should be at least an inch wide to prevent the animals from climbing the sides of the box or jumping out.

The entrance to the nest box is a one-inch round opening on one side near the bottom. This entrance can be closed from the outside of the box by means of a simple sliding door (Fig. 1). Boxes provided with two openings on opposite sides of the box, one to be used as a bolt hole by the inhabitants in the event of danger, were evidently not liked by the mice, because such boxes were rarely used by them.

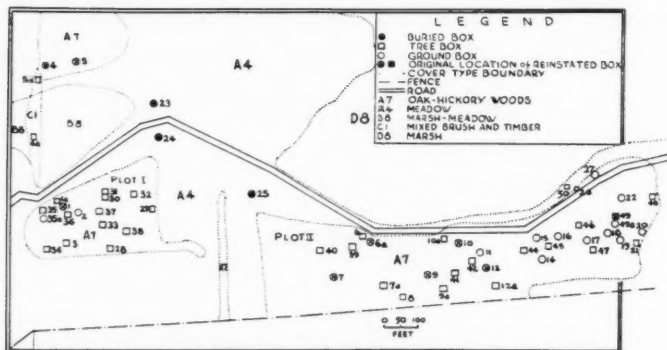


Fig. 2. Map of area studied, showing location of nest boxes.

A short wooden tunnel was attached over the opening of several of the boxes to simulate burrows. Some of the tunnels had right angle turns in them, while others were straight. Three of the boxes, designed to be buried underground, were equipped with long, sloping tunnels which would reach from the surface of the ground to the bottom of the box. Boxes equipped with tunnels were not used any more frequently than those without them. Nevertheless, the tunnels sometimes were useful in protecting the openings to the boxes from rain and especially from snow.

FIELD OPERATIONS

The study was conducted on the Edwin S. George Reserve, located near Pinckney, Michigan, about 25 miles northwest of Ann Arbor. Most of the operations were confined to two woodlots, 2 acres (Plot I) and 7.6 acres (Plot II) respectively, in area, and to the open field between them.

Fifty of the small wooden nest boxes, previously described, were put into operation between April, 1935 and May, 1937. Eleven of the boxes were later

relocated so that there was a total of 64 box locations (Fig. 2). In order that the effectiveness of the boxes under different conditions, as well as some of the factors entering into the selection of the nest by the wood-mouse, might be determined; and in order that there might be a greater possibility that the boxes would be used, the nest boxes were placed in many different situations. Some were placed on the ground within the woodlot; some were placed on the sides of trees; still others were fastened to the limbs of the trees; and three boxes were buried underground in the field adjoining the woodlots.

The nest boxes will be designated hereinafter as tree boxes or ground boxes, depending on whether they were located in a tree or on the ground. The ground boxes were placed at the base of trees, near logs or stumps, in brush piles, and under clumps of creeping juniper (*Juniperus horizontalis*). The tree boxes were placed in oak trees (*Quercus alba*, *Q. coccinea*, and *Q. palustris*), in hickory trees (*Carya lacinosa* and *C. ovata*), and in a maple tree (*Acer saccharum*). These trees ranged from 4 inches to 36 inches in diameter. Most of the trees were living, but a few were dead. The tree boxes furthermore were placed at various distances above the ground, varying from 3 feet to 30 feet.

When, in two instances, two nest boxes were located in the same tree, within a few feet of each other, only one box was occupied at a time, although both boxes were used by wood-mice at different times. Likewise, only one box was used at a time in two other instances when a tree box was supplemented by a ground box at the base of the same tree. One of these ground boxes was used once by a mouse after it escaped while being examined in the tree box. The other ground box and tree box was used interchangeably by one family group of wood-mice.

One nest box was placed in a tree located about midway between the two woodlots. The tree was standing in an old, brush-filled fence row, which formed a perfect avenue of passage for the mice from one woodlot to the other. This box was used rather frequently during the summer and fall.

Food, consisting of seeds and grains of several kinds, which at first was placed in some of the boxes, proved not to be necessary to attract the mice. Rather, the presence of food had a detrimental effect by attracting red squirrels and chipmunks, which often upset the boxes and frequently chewed rather large holes in them.

Nesting material of cotton batting placed in the boxes gave best results. A box which was not supplied with cotton was used only once, so far as could be determined, in all its history (November, 1935 to January, 1938), and then merely as a feeding station. Old nesting material was replaced by fresh cotton whenever it became wet or soiled from use.

Each animal found in a box was given an individual number and marked by means of toe clips and ear punches. Toes were clipped off by means of a pair of scissors and the ears were marked with a small poultry punch. By using both of the ears and clipping only one toe, it is possible to mark several thousand animals without repeating the numbers. The mice were marked without

anesthesia, because an animal carrying the odor of ether is often attacked by its companions.

A pair of rubber-tipped thumb forceps were used to handle the mice, which were usually caught by the tail or by the nape of the neck. The mice in the nest box were transferred one by one to a small cloth sack. Record was made of each previously marked mouse and the unmarked mice were numbered and marked. Then all mice were again placed in the nest box, and its entrance door reopened.

The original plan was to examine the boxes once a week every week of the year, in order that the movements and relationships of the animals occupying the boxes might be observed for all seasons of the year. By this procedure it was expected that the examinations would not be so frequent that the mice would be frightened away from the boxes. The plan was followed as nearly as possible until late in the course of the study, when, in an effort to determine the effect of more frequent disturbance, the boxes were examined every day for a period of one week during the month.

NUMBER OF WOOD-MICE TAKEN

During the course of the study 288 wood-mice were captured, of which 154 were adult and 134 were young. All mice about 45 days of age or older have been considered to be adult. Of the adults recorded, 89 (68 percent) were males and 65 (32 percent) were females. The difference in the number of the two sexes captured is probably due mostly to the tendency of adult males to travel further than adult females (Burt, MS and Townsend, 1936). Of the 134 juvenile mice captured, 71 (53 percent) were females in comparison to 63 (47 percent) males. This difference is not statistically significant.

Of the total number of wood-mice captured in the nest boxes 174 animals (60 percent) were taken more than once. Various individuals were recaptured from 2 to 25 times, the number recaptured becoming smaller as the number of times they were retaken increased. Approximately equal numbers of adults (89) and juveniles (85) were recaptured. In proportion to the total number of mice of each age group marked, however, more juveniles were retaken than adults, probably because of less timidity. It may be assumed that one of the reasons why still more young were not recaptured is that some of them were eliminated by predators while out foraging for food. Perhaps another reason why the juvenile wood-mice were not recaptured more frequently is that the young often wander out of the area in their search for an unoccupied territory (Burt, MS).

The data given above show that males and females and both adults and juveniles make use of the nest boxes provided for them. Because 60 percent of the total number of mice using the nest boxes repeated, some of them as many as 10 to 25 times, it seems probable that the mice used the nest boxes as frequently and in the same manner as their natural nest sites.

PROPORTION OF THE POPULATION TAKEN IN NEST BOXES

During a part of the summer of 1937 W. H. Burt was trapping and marking the wood-mice on the same plots where the nest boxes were placed. Opportunity is therefore given to compare the effectiveness of traps and nest boxes for determining the population of these mice.

On the two-acre plot (Plot I) between June and August Burt had records of 14 wood-mice. Between the period June to September all these mice made use of nest boxes except two males. Of these males, however, one was taken only once in a trap and the other only twice, and there is accordingly the likelihood that these animals were killed or had left the plot before they had a chance to enter a nest box. Three additional animals, two females and a male, were captured in nest boxes, but were not taken in Dr. Burt's traps. Each of these animals was recorded only once in a nest box; they may, therefore, not have had an opportunity to enter a trap.

On the larger woodlot (Plot II, 7.6 acres) Burt had records of 17 wood-mice during the trapping period of July 9-12, 1937. Ten of these failed to enter any of the nest boxes during the period July to October. However, six of these mice had previously been marked in nest boxes, so that only four (3 males and 1 female) of the number present on the plot in July failed to enter a nest box during the summer. In addition, one subadult male marked in a nest box in July failed to enter a trap during the same period.

The 1936 season gave almost identical results, except that lower figures were obtained for the nest box captures. This was to be expected, however, because there was a smaller number of boxes in each plot.

The evidence given above shows that nearly all the animals in a given area will, at least occasionally, make use of the nest boxes provided for them.

Social Life of the Wood-mouse

Certain aspects of the life history of the wood-mouse are well known, especially the animal's habitat preferences (Wood, 1910; Dice, 1922; Townsend, 1935; and others), its home range and territorial behavior (Burt, MS), and its breeding habits (Svihla, 1932). Very little is known of the more intimate aspects of its social behavior in nature. The following data, although far from being complete in many respects, are presented to help fill the gaps in our knowledge of the habits of this animal.

NEST SITES

The wood-mouse shows, in its use of nest boxes, a very definite preference for nest sites located above the ground. Tree boxes were used by 278 mice (16 of which escaped before they could be marked or before their marks were identified) 780 times as compared to 47 mice (6 escaped) taken 79 times in ground boxes. Seventeen of these individuals used both ground boxes and tree boxes. Each of the 33 tree boxes sheltered at least one mouse during the course of the study; but mice were captured in only 14 of the 23 ground boxes. Eight

other ground boxes, however, harbored mice at one time or another, as indicated by the presence of feces, food, or nests. One ground box was never used, so far as could be determined. The number of different mice which at various times occupied each of the 33 tree boxes during the nine months from May, 1937 to January, 1938, averaged more than five and ranged from 2 to 24 individuals. The largest number of mice to occupy at various times a single ground box was 9 individuals, but these were taken over a period of twenty-three months, from March, 1936 to January, 1938. The average number of different individuals (unmarked young excluded) using the ground boxes from time to time during the twenty-three month period of their service was about 1.8 mice per box.

Another indication of the preference for tree nest sites by the wood-mouse is the number of litters found in tree boxes as compared with the number found in ground boxes. Only three litters were taken in ground boxes while 34 were taken in tree boxes.

The evidence from the use of the nest boxes further seems to indicate that the wood-mouse prefers nest sites along the edge of the woodlot or in close proximity to the edge. Nineteen of the tree boxes were placed either on peripheral trees or within 25 feet of the edge of the woodlot, while 15 boxes were situated well within the woods. The average number of mice taken per peripheral tree box was 8.3 mice, taken on 8.5 occasions, while for the centrally located boxes, the average was 4.6 mice per box on 6.8 occasions. Because nearly twice as many mice were captured in boxes near the edge of the woods as were taken in the center of the woodlot, it seems reasonable to conclude that the wood-mouse shows a preference for nest sites located near the edge of the woods. The number of occasions on which the different boxes were used by mice leads to the same conclusion. The majority of the litters taken in boxes were first found in peripheral tree boxes, further indicating that the wood-mouse prefers nest sites near the edge of the woods.

There is no apparent correlation between the amount of use of tree nest boxes by mice and the size of tree, kind of tree, or height above the ground. Because so few mice were taken in ground boxes, it is impossible to correlate the amount of use by mice with the location of the boxes in relation to stumps, trees, brush, or creeping-juniper bushes. Neither is there any evidence that nest boxes of a certain size were used; the mice used large boxes as readily as small boxes, and also nest boxes of intermediate size.

The site of one natural nest was found in the branch of an oak tree (*Quercus palustris*), when a nest box was being placed in the same tree. The opening to this nest was a longitudinal crack on the upper surface of a branch which had rotted out, leaving an opening about one inch in diameter. The nest was not disturbed; therefore, it is not known how deeply into the heart of the branch this opening led, but from appearances the hollow was quite extensive. The opening to the nest was 7 feet above the ground in a tree 9 inches in diameter. This nest was used by mice from September 22, 1936 until February 5, 1937. So far as could be determined, the nest was not used after that time. This nest was located on the edge of the woods.

The amount of use of tree nest boxes in comparison to the amount of use of ground nest boxes seems, therefore, to show that the wood-mouse usually makes its home above the ground. In addition, the wood-mouse shows a preference for nest sites located near the edge of the woods. This rodent seemingly does not have any preference for nest boxes located in trees of different sizes or kinds; neither is there any apparent preference for nest boxes located a certain height above the ground. The one natural nest site found was in a tree near the edge of the woods.

SEASONAL VARIATION IN THE USE OF NEST BOXES

Their use of nest boxes indicates that wood mice seldom live on the ground during the summer; but during the winter, from November to March, a few mice nest on the ground. Of the forty-seven mice taken during two years in ground boxes, thirty-four were taken in the winter, the other thirteen being taken during the summer and fall months.

One condition which seemingly influences the ground-nesting of the wood-mouse in winter is the amount of snow. Apparently the greater the depth of the snow, the more readily will the mice nest on the ground. Twenty-two of the mice taken in ground boxes were taken during the winter of 1935-36, when the snow was piled up between two and three feet deep in some places in the woodlot. In the winter of 1936-37, with an almost complete absence of snow, only four mice were found in ground boxes. Eight mice were captured in ground boxes the winter of 1937-38, when the snow reached a depth of 6-8 inches. This was in spite of the short period of study (November to January).

The sparse indication given by the presence of feces, food, and nests in ground boxes, bears out the suggestion that very few mice live on the ground during the summer, but that they nest on the ground more frequently in the winter.

There is little evidence to support the suggestion (Wood, 1910) that there is a seasonal selection of nest sites near the edge of the woodlot. Although the one box located in the fence row was used only during the summer and fall months, and one box located on the edge of the woods was not used after November, another similarly located was used throughout one winter season by wood-mice. Johnson (1926:263) also has reported this species as frequently near the edge as in the middle of the woods at all seasons.

The wood-mouse then demonstrates an apparent preference for tree nest sites at all seasons of the year, but there is some tendency for individual mice to live on the ground in the winter when there is snow on the ground. There is seemingly little if any seasonal difference in preference for nest sites located on the edge or in the center of the woods.

CONSTRUCTION OF NESTS

Usually the mice were satisfied with the cotton batting provided as nesting material. Other articles, however, such as grass, leaves, hair, feathers, rags, and milkweed floss, have been added by the mice at various times to the cotton and

incorporated in the nest. On one occasion, an adult male mouse removed all the cotton from a box and then brought in milkweed floss and constructed his nest. When the nest was again examined, two weeks later, this male was absent, but three subadult males and one subadult female had taken over the nest and added more milkweed floss. Still later another set of mice, an adult pair and four young, occupied this nest but did not bring in any additional material, as far as could be determined.

An adult pair of mice occupied one box which was not supplied with cotton nesting material. These animals constructed a nest of dry leaves and grass. The leaves were cut into very small pieces.

The mice which used the natural tree nest site apparently constructed their nest of cotton batting, getting their supply from the nest box located within a few inches of the opening to the natural nest. When the mice were first discovered in September, they seemed to have a large enough supply of nesting material or were deriving it from some other source, for no cotton was taken from the box until October. During the latter part of October and through November, cotton batting placed in the box was removed almost immediately and because the opening to the natural nest site was eventually stuffed full, it was assumed that the mice in the natural nest were responsible for the disappearance of the cotton. By the end of November, the mice apparently had taken all they could use, as no more cotton disappeared from the box.

That cotton batting is used when available by the mice in their natural nests is evident, because cotton which was supplied to the nest boxes frequently disappeared and had to be replaced.

All the nests were constructed in essentially the same manner. The cotton batting was first shredded and then built into a globular form, hollow in the center, and with but a single opening. When the nest was in use the entrance was closed, and it also was frequently closed when the nest was not in use, as if the owner intended to return. Ordinarily, the opening to the nest faced the entrance to the box. Occasionally, however, it faced one side or the other, but in no case was it found to open toward the rear of the box. The nests were almost always completely roofed over, even in summer. Occasionally, the cotton had been brought up against the screen of the inner door leaving an opening of about one inch in diameter. In the winter months there was a tendency to build up the floor of the nest so that it was elevated above the top of the opening of the box. The nests made of leaves and milkweed floss were similarly constructed.

SANITATION

The fecal pellets of the wood-mouse are dropped promiscuously inside the nest boxes, and even inside the globular nest balls. The mice also urinate inside the nest boxes, but usually in the corners of the boxes, outside the nest ball. Even though the mice leave the cotton nest to urinate, the moisture remains inside the nest box and is soon absorbed by the cotton nesting material. The urine and fecal pellets together make some of the nests very foul and damp, therefore, in the winter portions of the nest are often frozen solid.

No natural nests have been examined but there is no reason to suppose that the wood-mouse is any more sanitary about its natural nests than about the nest boxes. Dice (1925:7) found some excreta in a *P. m. gracilis* nest.

Food was frequently eaten inside the nest box, and the remains, the shells of hickory nuts and acorns, were dropped on the floor. Eventually, the shells were packed into the nest material, thus rendering the bottom of the nest uneven and probably uncomfortable. The accumulation of nut and acorn shells hastened the soiling of the nest considerably.

Ectoparasites were not very evident, either on the mice or in their nests. A few lice (species not identified) were found on some mice; but only one nest seemed to be infested with these parasites. This nest was cleaned out, fresh cotton was put in it, and the lice were thus eliminated.

In spite of their unsanitary habits about the nest, all the mice captured were clean and the ventral surfaces of their bodies were immaculately white. It has been noted in the laboratory that captive mice spend much time on their personal toilet; apparently wild mice do likewise.

CO-RESIDENTS

Invertebrate animals other than ectoparasites were sometimes found in the nest boxes together with wood-mice. The nymphs of the wood-roach (*Parcoblatta pennsylvanica*) occurred in nearly all the tree boxes during the summer, sometimes in large numbers. The presence of the wood-roach seemingly did not interfere with the occupancy of the boxes by the wood-mice; nor did the mice seem to interfere with the roaches. Ordinarily the roaches were found above the inner door of the box, but regardless of whether the box was occupied by mice, the roaches would run down inside the box when the cover was removed. It is not known definitely whether the mice ever killed any of the roaches, but to all appearances these two kinds of animals lived in harmony.

Hornets (*Vespa maculifrons*) lived above the inner door of two different boxes at the same time the boxes were occupied by mice. The hornets had to gain entrance to their living quarters by the same opening which the mice used. Two wood-mice lived in the same box with hornets for a period of over a month.

Wood-mice occupied two nest boxes which were being used at the same times by carpenterants (*Camponotus herculeanus*). The ants were eliminated from both boxes in which this combination was found, by leaving the covers off as soon as the boxes were not occupied by mice. In both instances the mice were in the boxes with the ants only once.

Other animals were found in nest boxes on various occasions, but mice were not taken at the same time. In each instance it is doubtful whether any mice entered the boxes during the periods these other animals were present. A bumble bee (*Bombus* sp.) took over one box, a dead salamander (*Ambystoma maculatum*) was found in another, and on three occasions a tree toad (*Hyla versicolor*) was found in another box.

FOOD AND FOOD STORAGE

Acorns, hickory nuts, and corn (maize) were the only articles of food found in boxes used by the wood-mouse. Other types of food were probably brought into the nest and consumed, but either all such food was eaten, or the left-over particles were too small to be obvious. Although insects, such as the wood-roach and hornets, were sometimes found living in the same quarters as the wood-mice, there is no evidence to show that the mice killed and ate any of these insects.

When eating an acorn, the wood-mouse usually removes the cap, cuts the acorn in two around the middle on the mid-line, and then removes the meat from each half shell. Occasionally, the acorns are opened by shredding the shell down on all sides from the apex. Because the shells of the acorns were almost invariably destroyed, it was impossible to identify all the kinds of acorns consumed, but most of the kinds found on the George Reserve apparently were eaten. The red acorn, one of the most bitter, is apparently used for food as readily as any of the others.

Hickory nuts are always opened in the following manner: two holes are gnawed in the sides of the nut, opposite to each other. These openings usually occupy a little more than a quarter of the surface of each side. The openings are always made on the sides, crossing the longitudinal split in the nut; thus, when the openings are finished, the edge of the two halves of the kernel are exposed on both sides. Through these relatively small openings, the mice are able to obtain every bit of the food in each side of the nut. The mice eat both thin-shelled and hard-shelled nuts, both bitter and sweet nuts, all seemingly with the same readiness.

Traces of corn were occasionally found in some of the boxes. The wood-mouse consumes the entire kernel of corn, contrary to the habits of some other rodents, particularly squirrels, which eat only the germ and discard the remainder. Possibly the mice in the boxes derived their supply of corn from squirrel middens, carrying off discarded parts of kernels as well as whole kernels which had been dropped. The squirrels obtained the corn from cultivated fields adjacent to the Reserve.

The wood-mouse did not store any food in the nest boxes; but, from the condition of the empty shells, it was evident that the nuts and acorns were taken from some cache. The empty shells of both acorns and hickory nuts were found at all seasons of the year, but, at no season did the nuts show evidence of having weathered, nor were green nuts found during the summer. Therefore, both acorns and hickory nuts must have been cached somewhere. Many authors tell of finding the storehouses of the wood-mouse, but no one has mentioned finding the nest and storehouse in the same place.

PERIODS OF RESIDENCE

A wood-mouse seldom resides long in one nest box, but rather, it usually, though not always, leaves the box after a short period of residence, to reappear in the same box or in another box after a period of two or three weeks, or occasionally, of several months.

Of the 174 mice captured more than once in nest boxes only 16 lived in the same box for more than four consecutive weeks. Of these, four males and four females were each taken in the same box for four consecutive weeks; four males and one female were each taken over a period of five weeks; one male and one female were each taken over a period of six weeks; and one female was taken eight consecutive weeks in the same box. Each of two pairs from among the above mentioned mice remained in the same nest box for a period of five continuous weeks.

When the boxes were examined every day for a week, only three animals, an adult male, and an adult female and her one female offspring, were found to remain in the same box the whole week. Some of the mice remained in the box for two or three days and then disappeared, some returned after a day or two, but the majority of the mice were taken only once during the week of continuous examination.

More than half (9) of the mice which were taken in the same box more than four consecutive times were taken in the winter. Of the other 7 animals, three were repeatedly taken in the same box in the fall months and four were taken in the summer months. The three mice captured every day for a period of a week were taken in November and January.

Whether the wood-mouse normally changes its place of residence under natural conditions as frequently as indicated by these records, or whether these animals moved from the nest boxes because of being disturbed, is impossible to determine. However, because few mice lived in one location for more than a month, it seems logical to conclude that the wood-mouse changes its place of residence rather frequently.

LOCAL MOVEMENTS

Most of the movement involved when a wood-mouse changes its place of residence seems to be local, that is, within the normal home range of the individual. Of the 174 mice which repeated one or more times, 112 were taken in the same box each time, and 62 were taken in two or more boxes. All 62 of the mice using more than one nest box were retaken at one time or another within 200 feet of the original place of capture. Of these, 25 were adult males, 10 were adult females, 11 were immature males, and 16 were immature females.

Nest boxes which were more than 200 feet apart were used by five adult males, two adult females, three immature males, and one immature female. It will be noted that more adult males than females were taken in two or more nest boxes, both among those which showed only local movements and those which wandered more widely. This would be expected due to the greater wandering tendency of the males.

Those animals which were always taken in the same box demonstrated some local movement also, because most of these mice were not recaptured every consecutive week. Although it is impossible to tell how far the mice moved between visits to any one particular box, there must have been a certain amount of movement involved between nest boxes and natural nests.

The record of adult male No. 311 is a good example of the wanderings of these mice. This mouse was taken a total of 25 times, always in the same general region. He was first taken in box No. 3 (Fig. 3) on June 17, 1936, as a subadult. He remained in box 3 for 3 weeks, then on July 23 he was taken in box 28, about 90 feet away. August 11 and 18, and September 4 he was again taken in box No. 3. This animal did not make use of any box again until May 11, 1937 when he was taken in box 3; May 25 he was in box 34, approximately 90 feet away from box 3; June 8 he was in box 33, 160 feet from box 34 and approximately 70 feet beyond box 3. June 15 and 25 he was found in box 36, 95 feet from box 33. July 19 he was taken in box 37, 30 feet above the ground and 90 feet from box 36. August 3 he was again in box 36. Then he went back to box 37 on August 10. August 16 he was in box 3; August 17 in box 36; and on the 18th he was back in box 3. Between each of the last four dates this mouse moved his residence about 80 feet. He was not taken after August 18, 1937. Although this male used different nest boxes in 1936 than in 1937 he remained in the same local area.

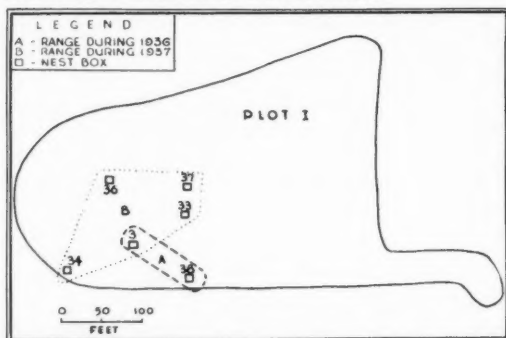


Fig. 3. Sketch map of the range of the movements of male No. 311 during two summer seasons, showing location of boxes occupied.

Nursing females make a practice of changing their place of residence rather frequently, taking their young with them. Females and their litters, of which the young mice ranged in age from one to 40 days old, were taken 34 times. Most of these young mice were between 15 and 40 days old. Because so many young between these ages were moved from nest site to nest site, it seems plausible to conclude that it is a regular procedure for females to move their young, perhaps several times during the nursing period. One female brought three litters into a nest box during one breeding season, the young of each litter being on each occasion from 18 to 25 days of age.

It is evident from the preceding discussion that a wood-mouse frequently changes its place of residence, but that most of the movements involved in the exchange of nesting sites is local. Adult males appear to move about more than adult females. Adult females with litters frequently change their place of residence.

DISPERSAL

The data are too few and inconclusive to determine whether or not the mice move their home sites more frequently or travel farther in summer than in winter.

Only 11 wood-mice were taken more than 200 feet from their place of first capture. Because of the importance of these for indicating the dispersal rate of the species the record of each of these animals will be given here.

One of the adult males moved, during a period of two weeks in summer, from a nest box in the woodlot into another box in the fence row, a distance of approximately 300 feet, and back to a nest box in the woodlot. Another adult male moved in November from the box in the fence row to a box in the woodlot, a distance of slightly more than 200 feet. Two other adult males travelled in the late fall, respectively, 280 feet in one week and 220 feet during a period of two weeks. One other male, trapped and marked in one woodlot by Burt during the fall, was taken the following July in a nest box in the other woodlot, a movement of over 1,500 feet. Except for this one animal, none of these mice moved very far.

One adult female, moved a distance of approximately 500 feet between July and November, from the nest box in the fence row to a nest box in the woodlot. However, her travel was accomplished sooner than the box records would indicate, for this mouse was trapped by Burt in the woodlot one week after she was taken in the nest box in the fence row. She was then only about half way between that box and the one in which she was captured in November. The other female travelled a distance of approximately 300 feet in one week in a similar change of nest boxes.

One juvenile female, which was taken on September 1 with her mother and siblings, was found November 3 in another box in the same woodlot, approximately 550 feet away. Two juvenile males from the same litter moved from one woodlot to another, a distance, for one mouse, of over 900 feet, and for the other, of about 750 feet. Both of these mice moved from the one woodlot to the other between November 3 and January 27. Another juvenile male moved, between November and April, a distance of slightly more than 200 feet, within the same woodlot.

Very few wood-mice, so far as these records show, move the location of their homes over a greater area than might be expected to be included in a normal home range. The longest movement, by an adult male, was over 1500 feet. One adult female was taken in nest boxes about 500 feet apart. A juvenile female moved about 550 feet. Two juvenile males moved respectively 900 and 750 feet. Six other wood-mice moved distances between 200 and 300 feet from their places of first capture. All the other mice which were captured in more than one nest box, were, as shown in a previous section, taken within a radius of 200 feet from their place of first record.

SEX RATIO

Eighty-nine adult males were taken in comparison to 65 adult females, while 63 juvenile males were captured in comparison to 71 juvenile females.

The amount of deviation from a possible 50-50 ratio is not statistically significant for either age class.

The ratio of males to females in the litters probably gives a more accurate statement of the sex ratio at birth. In 26 litters, with an average of 3.6 mice per litter, there were 48 males and 46 females. Groups of three or more mice, obviously of the same age but less than 45 days of age and those which were still being nursed by an accompanying female, were considered to be litters.

RELATIONSHIP BETWEEN ADULTS AND YOUNG

Few litters were born in the nest boxes, but litters of various ages were from time to time moved into the boxes; therefore it has been possible to record some of the relationships between the adults and young.

It has already been mentioned that groups of three or more mice, obviously of the same age but less than 45 days of age when first captured, were assumed to be litters. The age of these young mice was determined partly by the criteria given by Svihla (1932) and partly by criteria which are the results of my several years experience in handling mice of known age in the laboratory. Svihla states (p. 23) that young of the species *leucopus* when first born are naked, flesh colored, blind, and the pinna of the ear is folded down flat against the lower portion of the ear; on the second day after birth, the dorsal region of the body becomes darkly pigmented; and by the third day the pinna of the ear is unfolded. My observations show that in this species the hair becomes discernible to the naked eye on about the fourth day, and on the sixth or seventh day the young are completely haired. By the tenth or eleventh day, the young are able to walk by themselves, although they are still weak and crawl much of the time. At between 13 and 14 days of age the young of *novaboracensis* open their eyes (Svihla, p. 29).

After the eyes are opened it becomes extremely difficult to determine the exact age of the young wood-mice. However, until they reach the age of about 40 to 45 days, their age may roughly be estimated from their size. Young of this species are slightly less than half grown at the time the eyes are opened (14 days), fully half grown at about 18 to 20 days of age, and about two-thirds grown between 25 and 30 days of age. When they reach the age of 40-45 days it becomes almost impossible to separate the young from adults on the basis of size, but observations in the laboratory indicate that the young retain their gray juvenile pelage until about 40 to 45 days of age; at 45 days of age the buff of the adult pelage becomes apparent in the dorsal stripe; and by 60-75 days of age the adult pelage is almost completely attained.

A total of 37 litters were observed in the nest boxes, of which only five could possibly have been born there. Two of these litters were undoubtedly born in the nest boxes, because they were not more than one day old when found, and three other litters, ranging in age from two or three days old to six or seven days of age when found, probably also were born in the nest boxes. The other 32 litters were not born in a nest box, because they were over a week old when first found and they had not been present at the previous weekly examination. Seven litters were between 9 and 18 days of age, 16 litters were

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TABLE 1.—Association of sexes and age classes of wood-mice in nest boxes.
Number of times each combination was taken each month.

	Breeding season							Non-breeding season					Total
	March	April	May	June	July	August	September	October	November	December	January	February	
Number of seasons	2	2	2	2	2	2	2	3	3	3	3	1	
Mice captured	4	17	41	43	38	24	70	65	107	76	55	14	
Times taken	5	26	57	62	45	34	98	87	172	106	82	18	792
1 animal													
Adult male	3	9	5	10	9	14	25	16	15	7	9	2	124
Juvenile male				1	3	1	3	2					10
Adult female	2	11	1	3	2	2	3	4	9	8	16		61
Juvenile female				3	4	1	2	1					11
Undetermined					2	2	2		1	1			8
Total													214
2 animals													
Adult pair			4	1	1	6	1	2	19	17	7	3	61
Juvenile pair			1	1			3	2	1	1			9
Pair (female juvenile)			1	3			2	9					15
Males								21,2	3	1	3	1	10
Females		1						1 ¹		1			3
Total													98
3 animals													
Males								1					1
2 males + 1 female									1	1	2		4
2 females + 1 male									2	3	3	1	9
Total													14
4 animals													
2 males + 2 females										2			2
3 males + 1 female									1	1			2
3 females + 1 male									1	1	1		3
Total													7
5 animals													
3 females + 2 males										1			1
4 females + 1 male										1			1
Total													2
6 animals													
3 females + 2 males +													
1 undetermined											1	1	2
3 females + 1 male +													
2 undetermined										1			1
Total													3
Litter associations													
Female + litter			4	5	2	2	6	7	16	1			43
Male + litter			1				2		1	1			5
Pair + litter			2				2	1	5	1			11
2 males + 1 female +													
litter				2									2
Female + litter +													
male of previous litter ..				1									1
Female + litter +									2				2
previous litter													
Litters not associated													
with adults			1		1		1	1	4	3			11

¹ Juveniles.² 1 adult 1 juvenile.

between 18 and 25 days old, and 9 litters were between 25 and 40 days old when first found. The majority of these older litters were between 25 and 30 days of age when they were discovered in the boxes.

Twenty-eight adult females, assumed to be the mothers, were associated with 32 litters living in the boxes. One female was the mother of three different litters and three other females were the mothers of two litters each.

It is shown in Table 1 that litters were taken in the nest boxes a total of 75 times. They were, however, taken independently of their assumed mothers on only 16 occasions, on 11 of which they were not accompanied by adults, and on 5 of which they were associated with single adult males. All of the litters unaccompanied by an adult female were 20 days old or older and all but one were 25 days old or older. Most of these litters were between 25 and 30 days of age. Only one 20-day-old litter was taken alone. It was only during November and December that litters older than 40 days of age were accompanied by adult females. Because each litter was accompanied by an adult female until it was at least 20 days old and more usually 25 to 30 days old, and because none was accompanied by an adult female after it was 40 days old, except during the non-breeding season, it may be concluded that the young of this species are weaned between the age of 20 and 40 days and usually between the age of 25 and 30 days. The weaning age as here determined agrees with the observations of Svihla (1932:30) on laboratory reared wood-mice. Svihla found that, depending on several factors, the young of *noveboracensis* were weaned between the age of 22 and 37 days.

Until the young are near weaning age, it seems to be unusual for adults, other than the mother, to be found in the same nest with the young. Only one instance was recorded in the present study in which young less than 18 days of age were found with any adults other than their presumed mother. In this one instance, a female was taken with a 9-day-old litter and with one young male, about 37 days of age at the time, from her previous litter. This seems to suggest that until the young are about ready to be weaned, the mother, ordinarily, does not tolerate other mice in the nest with her young. Laboratory observations show that females with litters, though not always, force the male and the previous litter out of the nest when a second litter arrives.

On the other hand, after the young reach an age of about 18 days, or more frequently of 25 days or more, adult males are occasionally found in the same nest with the female and young. Of the 11 instances in which males were found associating with females and their litters, the young were 25 days old or older, except in three instances, one in November when a male was taken with a female and an 18-day-old litter, and two in June, when two subadult males, both obviously of the same age and possibly of a previous litter, were taken on two successive weeks with a female and an 18-day-old litter.

Single adult males were taken with litters on five occasions (Table 1). In all five instances, the males had previously been living with the litters and with the mother. Apparently the mother left the nest box, leaving the young and the adult male together. The male does not always remain with the litter and

weaned litters were taken alone on 9 occasions. After weaning, the litter usually breaks up and then, adult males frequently become associated with some of the young females. Adult males thus became associated with single young females on 15 occasions (Table 1). From the foregoing, it would seem that, although males frequently associate with litters and their mothers just about weaning time, males do not ordinarily continue to associate with the weaned litter, but they may attach themselves to single young females from these litters, after the litter breaks up.

Young males, after the family group has broken up, seldom associate with adults of either sex. The two instances of an association between adult females and young males have already been mentioned. In only two instances were young males found with adult males. Both occurred in October and in one instance a young male was found with a single adult male. In the other instance, one juvenile male was taken with two adult males.

It has been intimated during the discussion that the relationship between adults and young males may be slightly different in winter than during the summer and although it is not indicated in Table 1, litters do remain with their mother a much longer period of time in winter than in summer. For instance, one female and at least part of her litter remained together or in the same vicinity all winter long, until the beginning of the following breeding season. This female was taken with a litter 25-30 days of age on November 5, 1936. On November 12, she was taken again with five of these young (3 males and 2 females). On November 19, the female was taken with four of her brood (2 males and 2 females). The one young male was not taken again and it is possible that he was killed by a predator. All the mice disappeared then until January 14, 1937, when the old female reappeared with three of her brood and an adult male. On January 28, the old female was alone. On February 5, one of the young males and the adult male were taken together. On February 19, the two young females and two adult males were taken together, and also another wood-mouse which escaped. From that time on only single animals were taken in the nest box, until April 13, when the old female reappeared in a nest box with one of her daughters and another male. Neither the young mice nor the old female were taken after this date.

Other late fall litters have remained together or with the female throughout a portion of the winter. A female was living with one young female (18 days old) on November 3, 1937, and the two remained together through January 5, 1938. Another female was found with a litter of five young about 17 days old on October 6, 1937. All the mice disappeared until November 3, when the female appeared with a new litter of five young about 18 days old plus 3 of her previous litter. On November 10, she was taken with the three young of the former litter and four young of the latter litter. On November 15, she was with three young (2:1). The female then dropped out of the picture, but portions of the litters were taken on December 4 and on December 8.

During the summer, the longest time any part of a litter remained with the mother was about 37 days (one instance); on the contrary, in late fall and

winter litters occasionally remained with their mothers until they were between 45 to 60 days of age (3 litters).

Although the number of instances in which adult males were found with litters or with females and their litters, was not any greater in winter than in summer, the frequency of these associations is seemingly greater in winter. It is shown in Table 1, that 8 instances were found in the two month period from November through December, while 8 instances were also found in summer but the latter instances were found over a period of 6 months, from May through October. The two instances in which adult males were found with young males were in late October. This sort of combination did not occur earlier in the season.

In summary then, the use of nest boxes seems to indicate that of the 37 litters taken in nest boxes, very few were born in the boxes, but several litters were moved into the boxes shortly after birth. Further, litters are found with their mother until they are weaned, or until about 25 to 30 days of age. Other adults are seldom found with mice younger than 18 days of age, but after reaching this age and before weaning, adult males frequently become associated with young animals and their mother. After weaning, very few adults associate with litter groups, but as the litter breaks up, adult males occasionally become associated with single young females, but very rarely with young males. In winter the association between the young and the mother persists longer than in summer. Adult males, either related or unrelated become associated with litters more frequently and for longer periods in winter than in summer.

ASSOCIATION OF MALES WITH FEMALES

There is a different aspect to the behavior of the mice toward each other in the non-breeding season, extending from November through February, from that of the breeding season of March through October (Table 1). The table is composed of data secured from two years study, except for October, November, and December, which are represented by data for three years, and for February which is represented by only one year.

March marks the beginning of the breeding season, which extends through October. The length of the breeding season as indicated here is supported by the trapping records of Burt (MS). Burt found that some females of this species gave birth to young on or about the first of April. With a gestation period of about 23 days (Svihla, 1932) Burt's findings indicate that breeding begins early in March. Information from the use of nest boxes shows that some litters were born as late as about the middle of October, and several were born about the first of October. The non-breeding season, therefore extends from October to March. During the non-breeding season the vaginas of females are usually closed and the testes of males are usually abdominal in position.

During the breeding season, the wood-mice are usually found living singly, although occasionally certain animals associate with each other for a short period, especially as pairs. Of 43 animals taken a total of 62 times in June, the mice were taken singly on 17 occasions, as pairs on 7 occasions, and as

females with litters on five occasions (Table 1). This does not present a clear picture of the exact conditions, because 19 of these 43 animals were taken 24 times as members of litters. When these 19 animals and their mothers are excluded, it is then evident that the other mice usually lived alone. The remaining 19 mice were taken singly on 17 occasions and were found associating with each other on only 8 occasions. Three of the latter instances were associations between adult males and juvenile females, and one was an association of a male of a previous litter with a female and her new litter.

That the mice usually live alone during the breeding season is still more evident when the records of individual animals are presented in detail. One adult male was taken 10 times between May 18, 1937 and October 16, 1937. He was alone on 9 occasions and the other time he was with a female and her litter. An adult female was found twice alone and once with a single male. Another female was taken once with a male and her litter and twice with a litter. One male was taken 9 times and 7 of these times he was alone. On each of the other two occasions he was with a single female.

Although two or more animals occasionally live together during the breeding season, such associations are usually not very persistent. In one instance an adult male was taken with a female and her litter; the following week the male was found with the litter; the next week he was with two of the juvenile females from the litter; and the fourth week he was with only one of the juvenile females. After the fourth week, this male was not found with any of his previous associates. In another instance, an adult male was taken with two juvenile females and one juvenile male for three consecutive weeks. One juvenile pair from the same litter remained together for two weeks after the litter broke up. Very few associations composed of more than one animal of the same sex are formed during the breeding season, except family groups. There were only six instances in which such associations were found, and these were all found at the extreme limits of the breeding season. In April, two adult females were found together once, and on one other occasion in April two adult females and one adult male were found together. In October, two juvenile males, and two juvenile females, respectively, were taken together on one occasion each. On two other occasions, three males and two males, respectively were taken together. In each of the latter two instances one of the males was a juvenile.

During the non-breeding season, the relationship between males and females has an entirely different aspect from that of the summer season. During the winter, males and females are still found singly, but they are taken together more frequently than during the breeding season. Furthermore, combinations in which the sexes are unequally divided are occasionally found in winter.

It has already been mentioned that litters or parts of litters frequently remain together throughout the non-breeding season. If the litters break up, the various members usually become associated with other individuals, either males or females.

Most of the associations formed in the winter are between a single male

and female; however, in winter wood-mice often form associations with an unequal sex distribution. Twenty-nine of these associations are listed in Table 1 for the winter season, and besides these, there were thirteen other instances in which one animal escaped before its sex could be determined.

Pairs of mice, male and female, were found together on 48 occasions during the winter season. Two males were together on nine occasions and two females were found together on one occasion. Mixed groups of three were found on thirteen occasions. Mixed groups of four mice were found on seven occasions and in two of these instances, two males and two females were taken together. In two instances during the present study five animals were taken together, and in both instances there were more females than males in the group. On two occasions 6 animals were taken together, but each time one or two animals escaped, and the numbers of each sex in the aggregation was not determined.

From the evidence given above, it appears that during the breeding season wood-mice usually live singly. Occasionally, for a brief period, a pair may live together. During the non-breeding season the males and females frequently live alone. They, however, sometimes live together, ordinarily as pairs, but occasionally in aggregations in which the sex distribution may be unequal.

INBREEDING

The possibility of close inbreeding at times in the *noveboracensis* population on the George Reserve, is indicated by the data secured from the use of the nest boxes. For instance, an adult female and an adult male were taken together in February, 1937, and although these mice were not again taken together until May 11, it is possible that the male was the father of the two young females found with the pair at that time. The male was found with one of the young females on May 18, on May 25, and again on May 31. On the latter date the young female seemed to be in early pregnancy. Unfortunately this female was not taken again, and therefore it was not possible to check further on her condition. Although this female was only about 50 days old on May 31, she may have been impregnated by her presumed father. Clark (1938) found that females of this species have their first estrum, on the average, at about 46 days of age, and he records one instance in which a female conceived at the age of 39 days.

The above cited instance is the only one found by me in which there is a suggestion that a pregnancy resulted from the association of two wood-mice of close relationship. However, there are other instances in which presumed fathers associated with their presumed daughters a long enough period for mating to have occurred. In one instance a female and part of her last litter of the previous breeding season remained together all winter, and this association possibly may have resulted in a pregnancy of the mother by her son. However, in this particular instance, the female was not taken again after the last time she was found with her offspring in the spring and therefore, it was impossible to tell whether or not she was impregnated.

It is possible that some of the males and females of the same litter which

remain associated with each other for a considerable time also mate. A male and a female of the same litter, first taken on September 1, remained together in the same box until September 22. They both disappeared after the latter date, but at that time they were about 42 days of age, and unless the combination broke up when they left the nest box, it is possible that they produced young. The fact that litters in some instances, remain together all winter possibly could result in the first litter of the next season being the result of a union between brother and sister.

The above evidence seems to indicate that there may be a slight amount of close inbreeding in the wood-mouse populations. Matings may take place between father and daughter, mother and son, or brother and sister, for these combinations have been found in the nest boxes up until times when breeding may have occurred. However, no case of such close inbreeding has been positively proved.

Records of Other Species

Other small mammals, besides the wood-mouse have made use of the nest boxes from time to time. On several occasions, chipmunks (*Tamias striatus lysteri*) have run out of the ground boxes when they were opened, and one chipmunk was taken in a tree box. The one animal taken in the tree box was marked, but was not retaken. Other chipmunks escaped before they could be marked, therefore it can not be said whether the same individuals made repeated use of the boxes or not.

Meadow voles (*Microtus pennsylvanicus*) used one of the underground boxes on four occasions during the winter of 1936. A male *Microtus* was taken alone on December 22, 1936. The following week he was in the same box. Thereafter two new *Microtus* were taken, each one alone. Neither of the latter two mice were recaptured. Unfortunately, about the middle of February, runoff from a heavy rain filled the box with water which then froze rendering the box useless until April. No other *Microtus* were taken in nest boxes throughout the study. Wood-mice were never found in the nest boxes in association with either chipmunks or meadowvoles.

A total of 16 prairie deer-mice (*Peromyscus maniculatus bairdii*) were captured in nest boxes. All of these were captured either in the fall of 1937 or the winter of 1937-38. Because so few *bairdii* were captured, very little can be said concerning the home life of this species; however, the evidence from the nest boxes seems to indicate that *bairdii* does not differ very greatly in its life habits from *noveboracensis*.

The 16 prairie deer-mice were taken a total of 136 times, 14 animals each being recaptured from 2 to 13 times. One subadult pair of mice were taken together once in a box, another male and female were taken together twice, and the other 12 mice were each taken from 6 to 13 times.

With the exception of two *bairdii* of doubtful identification, which are not included in the total number recorded here, all the *bairdii* were taken in one

or the other of the three buried ground boxes, located in an open field between two woodlots (Fig. 2). The two doubtful animals mentioned above were taken in a ground box located in the edge of the woods during the winter of 1935-36. Unfortunately these two animals escaped at the time of first capture and were not taken again, therefore they were not positively identified. Because the winter of 1935-36 was a relatively severe winter, it is possible that these two deer-mice moved into the edge of the woods for the added protection the trees would afford them.

Bairdii used the same nest materials and constructed their nests in the same manner as *noveboracensis*.

The prairie deer-mouse is equally as unsanitary about its nest as the wood-mouse. Twelve of these animals lived in a buried nest box, the cover of which had caved in, and therefore the nesting material was usually found to be wet each time the nest box was examined, but the mice apparently were not daunted, for they continued to live under these conditions for some time. The prairie deer-mouse did not bring any food into its nest, so far as could be determined.

Apparently, the prairie deer-mouse does not change its place of residence, at least in winter, as frequently as does the wood-mouse. One group of five mice were taken together in October, 1937, and then disappeared until November, 1937, at which time they reappeared with 7 others. The following day only four mice were present, but the following week all 12 mice had returned, and except for two mice which visited another box on one occasion, all these animals remained in the same place at least until the termination of the study on January 29, 1938.

Very few data were secured on the movements of these mice. One mouse which was taken twice was absent on the intervening examination day. Two mice which moved from one box to another travelled a distance of about 150 feet in one night and then came back again during the following week. When these two mice moved the first time, they moved in a direct line from the one box to the other. This was determined by their tracks in the snow.

Male and female *bairdii* were always found together in the same nest, except on two occasions. In the one instance in which several males and females were taken together all the animals were probably related. In October, 1937, five animals were taken, evidently a pair and three offspring. A month later, these five animals reappeared with seven others which were obviously all of the same subadult age. Therefore, it may be assumed that this second group were a second litter of the original parents. This family group of parents and two litters remained together all winter long, except for one young which was probably eliminated by a predator. On March 6, 1938, this box was examined once again and it was found that 10 animals were still there, the original pair and 8 of the younger animals.

An aggregation believed to have been composed of a mixture of *noveboracensis* and *bairdii* was found together in a nest box in the field not far from

the edge of a woods on several occasions. Specimens of these mice were not saved and therefore identification as to species is unfortunately not positive, but it is felt that the field identifications are correct, since I have had considerable experience in handling live specimens of both species.

Discussion

It has been shown by this study that the wood-mouse frequently changes the location of its home. The movements involved in these changes of residence are probably within the normal range of the individual animals. In no instance were two families found living in the same nest box, nor were two families ever found living in different boxes in the same tree or in two boxes in close proximity. This observation is in accordance with the findings of Burt (MS) that each adult wood-mouse has a definite home range which is rarely changed during the breeding season, and that the range of the adult females rarely overlap.

The reasons for changes of residence are not fully understood. The periodic examination of the nest boxes by the observer undoubtedly disturbed the mice somewhat, but evidence has been presented that at least some of the mice were little, if at all, affected by this disturbance.

Th unsanitary condition of the nest after a period of use was probably an important factor in causing the frequent changes of residence. The nests become foul when in continual use. The need for frequent change of nest location is an especially urgent matter for females with young, for these family nests rapidly become unsanitary. Many litters were first moved into the boxes when the young were about 20-25 days of age, but some were younger. This indicates frequent changes of nest sites, especially by females caring for young. The frequent changes of residence by animals permit the nest to dry out between periods of use.

In winter, wood-mice of different ages and sexes frequently live together in the same nest, particularly as pairs, but occasionally in groups of three or more animals. Probably these groups live together for the added warmth afforded by several bodies. It has been observed in the laboratory that, particularly during the winter, all the *Peromyscus* in one cage usually huddle together in one nest. The extra warmth provided by a group must be an important factor in the survival of these animals during severe winter weather.

Also during the winter some nests become flooded or otherwise rendered unfit for occupancy. With this possible reduction in the most suitable nest sites, the mice might find it desirable to live in groups.

Beginning in March and becoming very evident in April, the winter aggregations of wood-mice break up. By the last of April or early May the mice are for the most part living alone, but are occasionally associated in pairs. Burt (MS) finds that some females of this species produce litters as early as the end of March, and that by the middle of April nearly all females have either had one litter or are pregnant.

The breaking up of the winter aggregation and the establishment of individual home ranges is undoubtedly correlated with the onset of the breeding season. It may likely be correlated with the change in the sexual glands leading to sexual maturity. When the sexual instincts are dormant the animals may be assumed not to be antagonistic to one another and they accordingly often live together in winter in small aggregations of mixed sexes. In the season of sexual activity, on the contrary, the animals are mostly solitary.

In the laboratory it has been generally observed that there is a great deal more fighting among adult *Peromyscus* during the breeding season than during the winter. When two adults, in breeding condition, of the same sex, and strangers to each other, are placed together in the same cage, much fighting usually takes place, even if both are placed in a cage which is strange to both. If one adult is placed in the cage of another adult, the stranger will usually be killed. Should several adult females be kept with an adult male in a cage, fighting between the females usually occurs when one of the females becomes pregnant. These difficulties occur less frequently in the non-breeding season.

A female with a very young litter does not tolerate the presence of a male in the same nest (Svihla, 1932). Nevertheless, a female will mate within 24 hours after the birth of her young if a male is present. In nature she must leave the nest for this purpose. In the laboratory the male is forced for several days to occupy a separate nest from that of the young, although his nest may be nearby in the same cage.

Male wood-mice are apparently promiscuous, contrary to Seton's (1920) statement. Males were found in nest boxes with several different females during one breeding season. Also, Burt (MS) has shown that the home range of one male may overlap the home ranges of several females, and that the male probably serves all the females in his range.

Litters of very young mice are always associated with an adult female, presumably their mother. Until just before weaning time, the mother presumably takes good care of her offspring, and probably fights off any intruders, even of her own species, which attempt to enter the nest. Observations in the laboratory both by Svihla (1932) and by the author show that females with newly born young seldom share their nest either with the male or with the members of a previous litter. So little is known concerning the family relations of small mammals that it is impossible to reach any definite conclusions as to why this apparent antagonism is set up between a male and a female which has a litter. It is probably instinctive and seemingly concerned with the protection of the young.

At weaning time (25-30 days) it seems to be the habit of the female wood-mouse to leave the young in the home nest and to seek a new nest for herself and her next litter. At weaning age the young mice are about full size and have probably already been travelling about with the mother for several days (Burt, MS). Whether this sort of behavior is common among small mammals is not definitely known, despite the common belief that animals usually force their young to leave the nest at weaning time. Deserting the young in the home

nest would certainly have its advantages for the young, because they would probably be more or less familiar with the immediate territory about their home. The familiarity with their surroundings probably aids the young in adjusting themselves to an independent life.

Desertion by the female of the young in the home nest and her selection of a new nest for the expected second litter would solve, temporarily, the problem of nest sanitation for the mother, and at the same time relieve her of the encumbrance of the previous brood, allowing her to devote her full time to the rearing of the second litter.

The young, during the summer, leave their nest box within, at the most, three weeks after weaning. The present study does not indicate how far the young travel. It is evident only that the young mice either move out of the territory or are eliminated by predators. As has been indicated, very few juveniles were taken more than three times (or for a maximum period of about 4 weeks) in the area studied.

Adult males frequently become associated with females and their litters just about the time the litter is to be weaned (25-30 days of age). After the female deserts the young, the adult male seldom remains with the litter as a group or with the young males, but he frequently remains associated with a single young female from the litter.

A desire on the part of the adult males to cultivate a new mate is offered as a possible explanation of this behavior. Clark (1938) shows that the average age of the first estrus in *Peromyscus leucopus* is about 46 days, and he records one animal that conceived at 39 days of age. Some of the associations between adult males and young females were of sufficient duration for some of these females to have become sexually mature.

The few notes on dispersal indicate that the wood-mice may travel considerable distances. The greatest distance in a direct line any wood-mouse is known to have travelled, in the present study, is about 1500 feet. This was by an adult male which moved from one woodlot to another during the winter. Most of the mice, however, did not move more than 200 feet from their place of first capture.

A certain amount of inbreeding would be expected in a population of wood-mice which is largely confined to a more or less isolated woodlot. Evidence from the records of individuals associated as pairs in the nest boxes indicate that close inbreeding may occur. Association in the summer between a presumed father and his daughter indicate the possibility of their mating. Associations in the winter between a presumed mother and her sons sometimes persisted long enough into the spring to have resulted in possible matings. Known brothers and sisters frequently remain together long enough to result in possible matings. Although actual proof of inbreeding has not been obtained, the associations which occur between parents and offspring and between litter mates are of a sort which might well result in mating and consequent inbreeding.

So little is known concerning the social relations of the smaller mammals

that it is possible at this time only to make a few comparisons between the social habits of the wood-mouse, as determined by the present study, and those of some other rodents. Vestal (1938) noted an apparent antagonism between male and female wood-rats (*Neotoma fuscipes*) during the breeding season. He states that males and females live alone, although they may live in the immediate vicinity of each other. Vestal noted further that when a female wood-rat with young attached to her teats ran into a house occupied by a male, the male left the house hurriedly. Beaver (*Castor canadensis*), on the other hand, seemingly do not have this sexual antagonism (Bradt, 1938). A male and a female beaver live together in the same house throughout the year. Beaver appear to be monogamous and, unlike the wood-mouse, adults, yearlings, and kits all live together in the same house. Before the birth of the young, the two-year-old beavers are literally "kicked out" of their home, and if they do not leave or can not leave, as in the case of the enclosed animals (Bradt, 1938:159), the two-year-old animals are probably killed.

It then becomes evident that the social life of the wood-mouse compares more closely with that of the wood-rat than with that of the beaver. This is probably to be expected because the wood-mouse is more closely related taxonomically to the wood-rat than to the beaver. It has also been shown above that the social life of the prairie deer-mouse, so far as the observations go, is similar to that of the wood-mouse. These two mice belong to different species of the same genus, and therefore are very closely related.

Summary

Artificial nest boxes placed in the woods and fields and examined at regular intervals have given much useful information about the home life and social habits of the wood-mouse (*Peromyscus leucopus noveboracensis*).

The nest of this mouse in southern Michigan is usually placed in a tree and more frequently near the outer edge of the woods than in the interior of a woodlot. Arboreal nest sites are used slightly less frequently in winter than in summer, and terrestrial nest sites more frequently in winter than in summer.

These mice are very unsanitary in and about their nests. No food was stored in any of the nest boxes. The wood-mouse frequently changes its place of residence, probably in part because of the unsanitary condition which the nest rapidly acquires.

In winter, wood-mice of different sexes and ages may live together. Probably these mice live together in part for the added warmth of several bodies and also perhaps because of a possible scarcity at that season of suitable nest sites. In summer, wood-mice are mostly solitary. The antagonisms between individuals of the same sex and at times between those of different sex are correlated with the onset and development of sexual activity in the spring. In mating habits, wood-mice are apparently promiscuous. Females with very young litters do not tolerate the presence of a male in the same nest. At weaning time, the mother wood-mouse deserts her young, leaving them in the old

nest. An adult male wood-mouse frequently becomes associated with a young female soon after she has been weaned.

The few data available on dispersal indicate that a single wood-mouse may travel as far as 1500 feet, but only a few of the mice moved more than 200 feet from the place of their capture. There is some indication that close inbreeding may at times occur in the wood-mouse population. Field identification of mice indicates the possibility of the wood-mouse and deer-mouse occupying the same nest, at least in winter.

The social life of the prairie deer-mouse, so far as the few observations go, is closely similar to that of the wood-mouse. The type of social life exhibited by these small mammals seems to correspond most closely with that of the other rodents which are closest in taxonomic position.

REFERENCES

- BRADT, GLEN W. 1938—A study of beaver colonies in Michigan. *Jour. Mammalogy* 19:139-162.
- BURT, WILLIAM H. Manuscript. The home range and territories of the Wood-mouse.
- CLARK, FRANK H. 1938—Age of sexual maturity in mice of the Genus *Peromyscus*. *Jour. Mammalogy* 19:230-234.
- DICE, LEE R. 1922—Some factors affecting the distribution of the prairie vole, forest deer mouse, and prairie deer mouse. *Ecology* 3:29-47.
- 1925—The mammals of Marion Island, Grand Traverse County, Michigan. *Occ. Papers Mus. Zool. Univ. Mich.* 160:1-8, 1 pl.
- JOHNSON, M. S. 1926—Activity and distribution of certain wild mice in relation to biotic communities. *Jour. Mammalogy* 7:245-277.
- SETON, ERNEST THOMPSON. 1920—Notes on the breeding habits of captive deer-mice. *Jour. Mammalogy* 1:134-138.
- SVIHLA, ARTHUR. 1932—A comparative life history study of the mice of the Genus *Peromyscus*. *Misc. Pub. Mus. Zool. Univ. Mich.* 24:1-39.
- TOWNSEND, M. T. 1935—Studies of some of the small mammals of Central New York. *Roosevelt Wild Life Ann.* 4:1-120, 8 pls., 22 figs.
- VESTAL, EDEN H. 1938—Biotic relations of the wood rat (*Neotoma fuscipes*) in the Berkeley Hills. *Jour. Mammalogy* 19:1-36.
- WOOD, FRANK E. 1910—A study of the mammals of Champaign County, Illinois. *Bull. Ill. State Lab. Nat. Hist.* 8:501-613, Illus.

Pollen Spectra as Time Markers¹

J. E. Potzger

A few years ago the cranial bones of an extinct moose, *Cervalces* sp?, were found in the peaty deposits in the valley of Potato Creek, near North Liberty, St. Joseph county, Indiana. A full description of this rare fossil was given by Gazin (1938). The bones are now in possession of the U.S.N.M., No. 15,494. The finder of the skull, Mr. Alton Bernhardt, of North Liberty, collected with the skull some of the soil in which the bones lay embedded and gave it to Dr. Marcus Ward Lyon, of South Bend, Indiana, who in turn sent it to the writer for pollen analysis and a possible determination of the age of the skull.

Slides were prepared in the usual manner of preparation of peat for pollen analysis. The soil contained primarily plant remains with a slight admixture of quartz sand. Microscopic examination showed pollen not very abundant but in excellent state of preservation. A count of 200 grains, the customary number counted in such tabulations, yielded results as shown in Table 1.

TABLE 1.—Pollen spectrum from soil collected with cranium bones of *Cervalces* sp? in the valley of Potato Creek, St. Joseph county, Indiana.

Genus of tree	% pollen present
Abies (Fir)	38.00
Picea (Spruce)	36.0
Pinus (Pine)	6.5
Larix (Tamarack)	2.5
Quercus (Oak)	8.0
Salix (Willow)	2.5
Betula (Birch)	2.0
Unknown	6.0

Pollen investigations to determine forest succession and migrations have in late years become increasingly more popular in the United States, but seldom has a pollen spectrum been used to estimate the possible age of animal remains embedded in peaty soil. In such a correlation it must be borne in mind that animal bones may not occupy the stratum where death occurred, but perhaps sank from a higher to a lower stratum. This is especially possible in bogs or boggy river valleys where periodic flooding might have made the soil too soft to carry heavier objects.

Considering the pollen spectrum from the Potato Creek soil per se we find that the bones of *Cervalces* were embedded in peat deposited at a time when the surrounding forest was strikingly boreal, for three-fourths of the pollen is from spruce and fir with an admixture of tamarack and pine. How-

¹ This is contribution 112 from the botanical laboratories of Butler University, Indianapolis, Indiana.

ever, oak had made its appearance (Table 1), which in Indiana bogs is a definite horizon marker of a moderating climate. If we compare pollen spectra from bogs and lakes in northern Indiana we find similar pollen percentages for the leading genera at a time when four to five feet of deposits had accumulated. If we compare sediments totalling four to five feet with the superposed layers bringing us to the present, they would comprise about $\frac{1}{9}$ to $\frac{1}{10}$ of the total deposition customarily found in bogs and lakes of Late Wisconsin glaciation in Indiana. The question now arises as to what this would mean in terms of years. In such a correlation one realizes that time is a relative thing, hooked up with events which are definitely located. In Europe pollen analyses have been used to place various cultural and agricultural advances. Using a stone dagger found in a bog as horizon marker for the Neolithic age, as well as for a stratified alluvial deposit along the Baltic and North Seas, Werth (1936) places the age of a prehistoric plow, excavated from the lowest level of a high moor, at about 6,000 B. C., or into the close of the Neolithic age, while Rytz (1935) places the age of this same plow into the bronze age, approximately 4,000 B.C., because in the pollen spectrum associated with other Neolithic age artifacts *Fagus* was absent while *Fagus* pollen was present in the soil associated with the plow.

In the present investigation we have three sources of evidence which can be used as time markers, viz., rate of accumulation of sediments, varves in clay deposits known definitely to have been deposited by glacial melt waters, and the present rate of cutting in the Niagara gorge compared with the amount of cutting since glacial retreat. All three markers, however, are subject to error of estimation, as the figures in tables 3 and 4 well show.

Using the recession of the Niagara gorge and of the St. Anthony Falls as criterion, Cleland (1925) estimates the permanent retreat of the Wisconsin ice sheet as between 12,000 and 20,000 years. Of course, to this would have to be added the time during which the ice retreated from its southern limit to the Niagara gorge. Antevs (1928) estimates the beginning of the retreat as between 30,000 and 40,000 years. Wilson (1938), studying varved sediments from Sandusky Bay, counted 12,223 varves and believes that these strata were laid down from soil in the melting ice, and he is of the opinion that the varves represent the minimum time during which the glacier had retreated from the western to the eastern end of Lake Erie, a distance of approximately 255 miles. This would mean an average retreat of about 110 feet annually. Antevs (as quoted by Miller, 1928) studied varves in clay deposits and came to the conclusion from this line of evidence that the last glacier receded a distance of 185 miles in western New England in 4,100 years, or an average of 240 feet annually. This would be more than twice the rate estimated by Wilson for Lake Erie. It will, perhaps, be of some significance to compare the figures of these computed recessions with actual measurements of glacial recessions during recent times, including the year 1937. There appears to be no doubt that the climate of our north temperate and Arctic latitudes is becoming warmer and glaciers are retreating, as shown by Cooper (1923, 1931), Griggs (1914, 1934) and more recently by Matthes (1938,

1939) of the U. S. Geological Survey. The latter author quotes the figures on recession as shown in Table 2.

TABLE 2.—Averages of recession of present-day glaciers in North America.

Location	Glacier	Years	Annual av. recession in ft.
Mount Baker	Easton	28	176
Mount Baker	Coleman	26	86
Mount Rainier	Nisqually	19	70
	Emmons	7	66
Rocky Mountain Nat. Park	Tyndall	5	34
Alaska	Valdez	13	70.6

The above figures are closer to the estimate made by Wilson than the one by Antevs but the figures also indicate that it is not safe to generalize too much since geographical location will be a vital factor in wastage of ice masses; one can, however, consider the estimates of these authors as very conservative, and rather too low than too high in their computation of the time element.

Miller (1928) estimates on the basis of Antev's figures, that the Wisconsin ice sheet required 12,000 years to retreat from the southern limits (somewhat south of Logansport for central Indiana) to the Niagara gorge. He further estimates on the basis provided by the present known rate of cutting by Niagara Falls, that 25,000 years have passed since the gorge was free of ice, which would make a total of 37,000 years. Again, we point to the possibility of large discrepancy in such estimations.

We are not much more fortunate with computing time elapse on basis of accumulation of organic deposits in lakes and bogs. Three published records of estimates of time represented by accumulation of peat are given in Table 3.

TABLE 3.—Estimate of time necessary to have a given amount of peat accumulate.

Author	Time in yrs.	Depth in inches	Yrs. for 1 ft.
Soper and Osbon (1922)	100	1 to 2	600 to 1,200
Sears (1932)	25	1	300
Dachnowski (1912)	200	12	200

The average amount of deposition in Indiana bogs is between 32 and 40 feet. The lapse of time since filling began would vary with the unit of time (Table 3) which we would accept and apply. If we follow Sears, and strike an average between 32 and 40 feet of accumulation at 35 feet we would arrive at 10,500 years, if we follow Soper and Osbon it would be 21,000 to 42,000 years. This latter figure more closely agrees with computations based on counts of varves and recession of Niagara Falls. Taking the various estimates of time and applying them to "average" accumulation of sediments in Indiana bogs, we have the following possibilities of estimating the time since the death of Cervulces:

Miller's estimate (based on varve counts and recession of Niagara gorge) 37,000 years
Deducting from this the time required by the glacier to retreat from the
southern limits to the North Liberty area (about 57 miles)..... 1,250 years

This would make the lapse of time since the North Liberty area has been free of ice35,750 years
 If we assume that the average accumulation of sediment during that time to have been 35 feet, one foot would represent approximately 1,021 years. If we further estimate that about five feet of sediment had accumulated when Cervalces died it would total 5,105 years
 This would make the total lapse of time since the death of the moose30,645 years

TABLE 4.—Various estimates of time during which thirty-five feet of sediments could have accumulated, minus the time represented by accumulation of five feet of sediment as computations of lapse of time since the death of Cervalces.

Author	Time in years
Dachnowski	6,000
Miller, based on varve counts and recession of Niagara gorge	30,645
Sears	9,000
Soper and Osbon (one inch to century)	36,000
Soper and Osbon (two inches to century)	18,000

A mere glance at Table 4 will show that the figures are the product of a little fact multiplied by estimate. The only approximate accurate time element is that represented by location of the cranial bones compared with accumulation of sediments to the present, i.e., eight to ten times as much time has apparently passed since the death of Cervalces to the present than since deposition began to the time of death.

REFERENCES

- ANTEVS, ERNST. 1928—The last glaciation. Am. Geo. Soc. New York.
 CLELAND, H. F. 1925—Geology, Physical and Historical. Am. Book Co., Chicago, Illinois.
 COOPER, WM. S. 1923—The recent ecological history of Glacier Bay, Alaska. Ecology 4:93-128; 223-246; 355-365.
 ——— 1931—Third expedition to Glacier Bay, Alaska. Ecology 12:61-95.
 GAZIN, C. LEWIS. 1938—A cranium of the extinct moose, Cervalces, from the Quarternary of Northern Indiana. Am. Midl. Nat. 19:740-741.
 GRIGGS, ROBERT F. 1914—Observations on the edge of the forest in the Kodiak region of Alaska. Bull. Torr. Bot. Club 41:381-385.
 ——— 1934—The edge of the forest in Alaska and the reasons for its position. Ecology 15:80-96.
 MATTHES, FRANCOIS E. 1938—Report of Committee on glaciers. Trans. Am. Geophys. Union.
 ——— 1939—Report of Committee on glaciers, April 1939. Trans. Am. Geophys. Union.
 MILLER, W. J. 1928—Introduction to Historical Geology. D. Van Nostrand Co., Inc., New York.
 RYTZ, WALTER. 1935—Der Älteste Pflug der Welt: in Deutschland. Ber. Deutsch. Bot. Ges. 53:811-818.
 SEARS, PAUL B. 1932—Postglacial climate in Eastern North America. Ecology 13:1-6.
 WERTH, E. 1936—Bemerkungen zu Rytz: Der älteste Pflug der Welt. Ber. Deutsch. Bot. Ges. 54:15-26.
 WILSON, IRA T. 1938—The nature, distribution and quantitative sediment in the upper part of Sandusky Bay. Div. of Conservation of Ohio, Bulletin.

Book Reviews

THE NEW SYSTEMATICS. Edited by Julian Huxley. Clarendon Press, Oxford. 1940.
viii + 583 pp. \$6.00.

One evidence of the increasing interest in the problems of taxonomy is the appearance of this book, sponsored by the British "Association for the Study of Systematics in Relation to General Biology." As the editor says in his introductory essay (one of the best parts of the whole volume) taxonomy has "become one of the focal points of biology" and the remainder of the book is made up of 21 separate papers loosely and somewhat irregularly grouped around this focal point. Less than a third of the authors could be called taxonomists; the bulk of the work has been written by experimental workers of one kind or another. It is, therefore, a stimulating book, as stimulating as would be a volume on "The New Genetics" written mostly by taxonomists and biochemists. It might even be called illuminating in the sense that the opinions of experts are usually most self-revealing when they discuss subjects outside the field of their special knowledge.

There is an excellent discussion of hybridization in the higher plants by Allan of New Zealand, an outstanding chapter on natural versus artificial classification by T. A. Sprague, and a short discussion (by J. S. L. Gilmour) of the philosophic basis of taxonomy which could be read with profit by any biologist. Dr. W. B. Turrill contributes a comprehensive summary of the experimental techniques which he and a few others have used with conspicuous success. There is an essay on Taxonomic Species and Genetic Systems by C. D. Darlington, the cytologist, which is the clearest and most concise exposition of his cytogenetical philosophy which has yet appeared. It should be read carefully by every cytologist who is interested in cyto-taxonomy; I doubt if the average taxonomist would understand very much of it, but attempting to do so might be good mental discipline. There are several chapters stressing the coordination between modern genetics and taxonomy and chapters on the special problems of insects and of cultivated plants.

One of the best features of the book is that it is concerned with taxonomy as a whole; not merely the taxonomy of the higher plants, or of the insects, or of mollusks. The systematist who reads the book may well gain as much stimulus from considering the problems and techniques and points of view of his fellow systematists who work with different organisms as from the work of experimentalists who study the same organisms for a different purpose.

My most fundamental objection is that the volume as a whole ignores much of the recent work in its special field. A book of nearly 600 pages on the new systematics, which has 44 references to the work of Dobzhansky, 20 to Muller, and 17 to Sturtevant (nearly all of these on the genetics of *Drosophila*) and which at the same time passes over the work of the only laboratory in the world devoted to the experimental study of taxonomy is obviously unbalanced. Not that the *Drosophila-kunde* is unimportant. Far from it. It is certainly today the most stimulating influence coming into taxonomy from the outside. But a volume devoted to the new systematics, if there be any such subject, should at least survey the field. Yet outside of Dr. Turrill's excellent discussion of new techniques there is no such summary. There is, for instance, not a single mention of the brilliant work of Stebbins on apomictic plants, none to Pickford's on earthworms, none to Mayr's work on birds and only one to that of Stresemann (birds). There is no reference to the work of Eric Hultén, either in connection with his ecological and floristic studies in Kamchatka or to his analysis of the circumboreal flora. There is only a passing reference to the monumental work on *Crepis* by Babcock and his co-workers. One of the few laboratories in the world which is really equipped to carry on work in experimental taxonomy is that maintained, purely for

that purpose, by the Carnegie Institution at Palo Alto, California. The volume ignores almost completely two decades of work from this laboratory; there is a passing reference to H. M. Hall and a single one to Clausen and Keck. It is, to revert to our original comparison, as unbalanced as a book on the New Genetics which had fifty references to the taxonomy of the higher plants, half that many to experimental embryology, and only one or two to *Drosophila*.

In a book of this sort there is to be expected a great deal of difference in opinion and in points of view. That the work as a whole is as well integrated as it is, is a tribute to the very great ability of the editor. However, one cannot read it through without wondering what some of the contributors thought of some of the other chapters. Some indication of this difference in attitude may be gained by quoting two definitions of taxonomy. Sprague begins his chapter with a definition to which I think most taxonomists would assent: taxonomy is the "scientific classification of the different kinds of living organisms according to their proved or inferred phylogenetic relationships." Huxley, however, defines the fundamental problem of systematics as "detecting evolution at work" and its chief question as to how discontinuity is introduced into the biological continuum." This may well be the aim of natural history or of certain fields in biology, but I—for one—doubt if there are many taxonomists who ever think about their work in this light. Certainly the ablest plant taxonomists with whom I am acquainted are much more interested in "what" than in "why"; in the results of evolution and how to order them up than in hypothesizing the forces which produced those results. A number of us certainly are working in a new field which borders on taxonomy on one side, on cytogenetics on the other, and which apparently falls within the vast claim staked out by the founders of ecology. Whether that field is now or ever will be a legitimate part of the concern of taxonomy is a very moot question. In fact, if I were to add a chapter to the book its title might be, "Is there, or should there be, a new systematics?"—EDGAR ANDERSON.

CATALOGUE OF FORAMINIFERA. By Brooks F. Ellis, Ph.D., and Angelina R. Messina, M.A. The American Museum of Natural History, New York City, N. Y. 1940. 30 volumes, over 30,000 pages. \$100.

The Catalogue of Foraminifera is the initial publication of the Micropaleontological Department of the American Museum of Natural History under the direction and supervision of Professor Brooks F. Ellis of New York University and Angelina R. Messina, formerly of Columbia University. A staff of 125 specialists in micropaleontology and other phases of the work have been employed continuously for more than six years in producing this voluminous compilation.

These volumes contain 30,000 pages of text and illustrative material on all the genera and species of Foraminifera, available in the libraries of this and other countries. Each generic transcript consists of the original reference and description, the type species as designated by the author and a chronologically arranged list of subsequent references. Each species is represented by the type reference, type figure, a transcript of the original description, the age of the type specimen, the depository of the type specimen whenever it is known, and a chronologically arranged list of subsequent references. All genera and species are alphabetically arranged. Each volume is bound firmly in a ledger type post binder, making it a loose leaf file into which additional sheets can be inserted in their proper order as they are received. The last volume of the set consists of synonymic changes in the names of the genera and species. To many students of Foraminifera this one will be extremely useful.

The entire publication of 30 volumes will be mailed to those who apply for the *Initial Membership* in the Department of Micropaleontology and pay the required fee of \$100.00 and mailing charges. A permanent staff of specialists and artists will be maintained to extend this work to the current publications as well as to begin the complete compilation of the generic and specific descriptions, with figures of the types and related data on other groups of microfossils. This later information will be avail-

able to the members who have subscribed for the *Initial Membership* and supplemented it with a *Continuing Membership* or *Active Membership*. Even personal request of the members for micropaleontological information or service will be given proper attention for a very nominal fee.

The American Museum of Natural History by this plan has made available to the students of Foraminifera not only the original material from publications that are very rare and in many cases almost impossible to obtain, but also the genera and species that appear in the numerous domestic and foreign journals and magazines.

—H. N. CORYELL.

LEWIS AND CLARK: LINGUISTIC PIONEERS. By Elijah Harry Criswell. Columbia, Missouri, 1940. The University of Missouri Studies vol. 15, no. 2, ccxi + 102 pp. \$1.25.

Professor Criswell's study is a heartening reminder that, amid the rather general apathy towards American philology in our universities, some valuable investigation still goes on. Professor Criswell continues the examination of the linguistic sources and processes in American English initiated at the University of Missouri by Professor Robert L. Ramsay and his associates. It is quite appropriate that an institution situated in a section in which American speech has been most creative and lusty should foster such investigation.

This volume "attempts to present the results of an examination of the vocabularies found in the extensive journals kept by members of the momentous Lewis and Clark Expedition of 1804-1806." It falls into two parts, "Introduction" and "Lexicon," and the Introduction is in turn divided into a section entitled "Things: The New World of the Explorers" and a complementary section labeled "Words: Fitting the Language to the New World."

Under the first heading in the "Introduction" the author has given a readable summary of the itinerary of the expedition, a sketch of the personality of the leaders, and a somewhat detailed account of their experiences, illustrated by well-chosen excerpts from the *Journals*. He has dealt in systematic fashion with the equipment of the explorers, their contacts with various Indian tribes, the dress, habitat, and customs of the aborigines, the fauna and flora of the new country, and its topography. At the end of each phase of the discussion, he has appended a list of words used by the explorers to describe that phase. This section concludes with zoological and botanical indexes of standard scientific nomenclature opposite to which are ranged the homely corresponding terms of the explorers, in which, by the way, the *Journals* seem to be especially rich.

This part of the study has an interest, independent of its purely linguistic value, for the general student of American culture, as well as for the anthropologist, zoologist, and botanist. We become acquainted with the efficient but quaintly pedantic Lewis, whose style is generally both circumlocutory and prosy but who is capable of hitting off such a happy malapropism as "Amorite" for an amorous man; with the more terse and graphic Clark, who characterizes one Indian dialect as "a gurgling kind of language spoken much thro the thought." We appreciate Whitehouse's linguistic note that they met a large canoe loaded with Indians, one of whom "could curse some words in English." We may even admire the fine indifference of all members of the party to the demands of conventional orthography. And for those interested in American botany and zoology there is an abundant harvest.

Of more specialized interest is the division entitled "Words." Here against the background provided by the first section Professor Criswell studies the methods by which Lewis and his companions solved the problem of labeling what was new to their experience. Here we see language in the making; we watch the final step in the mastering of a new environment, the processes by which man creates a medium through which to communicate his discoveries. The methods used by the explorers were age-old devices: they adopted rather reluctantly a few Indian and French words; they adapted

many already familiar words by extending their meaning; they invented a large number of new combinations; and finally they struck off an occasional onomatopoeic coinage.

Professor Criswell classifies the vocabulary pretty much according to the plan used by Professors Ramsay and Emberson in *A Mark Twain Lexicon*. Using the O E D as a basic authority, he divides the words into twelve classes, such, for example, as Americanisms (in the O E D); acknowledged Americanisms (not in the O E D); disputed Americanisms; unrecorded Americanisms (general terms); unrecorded Americanisms (zoological and botanical); adoptions (terms recorded in the O E D but only since 1700).

The "Lexicon" lists 1859 terms. Each word or combination is followed by a symbol indicating to which of the twelve categories it belongs, after which comes the quotation or quotations from the *Journals*, and finally the lexicographical information, that is, the status of the term, if it has been recorded, in the O E D or in other authoritative lexicons.

Anyone who examines the volume will be struck at once by the fact that the "Introduction" occupies more than twice the space needed for the "Lexicon." Given the plan of analysis used by Criswell, perhaps home such inequality was inevitable. Nevertheless, the impression remains that the author has succumbed to a tendency, common enough in this type of research, to over-elaboration of the analytical machinery. One grows slightly bewildered in the face of classification and re-classification. In such elaborated analysis, the investigator risks the operation of the law of diminishing returns.

The emphasis in this study should be, it would seem, on the number and character of the new words contributed. If this be so, one may doubt the vital value, for example, of classifying the terms which had been in use during the century preceding the Expedition. Again, the division of unrecorded Americanisms into two classes, of general and of zoological and botanical terms, seems slightly gratuitous.

But it is safest to err on the side of completeness, no doubt, and one hesitates to find fault with a work which has turned up 703 words hitherto unrecorded in any dictionary and 1004 words which first appeared in the *Journals*. If on casual examination the "Lexicon" seems at first glance lacking in the novel and picturesque character which Mr. Mencken has taught us to expect in the "American" language, it should be remembered that many of the familiar terms have become familiar during the last century, that the writers of the *Journals* were not creative writers but practical explorers, and finally that some of the seemingly familiar terms are not familiar in the peculiar sense in which the explorers used them. But the lexicon does contain its graphic words. One need only cite the combination *prairie dog*, suggested by the habitat and barking of the squirrel-like animal to which Clark applied it; or *whistling swan*, a term suggested by the peculiar noise made by this bird; or *mule deer*, named for the resemblance of this animal's head and ears to those of our once familiar beast of burden, or *chittediddle*, an onomatopoeic formation.

It is to be hoped that Professor Criswell's study will point the way to further researches into material of a like nature. Lacking, as we do in America, numbers of local antiquarians, so numerous in a country like England, we must depend largely on university projects to supply the stores out of which American dictionaries and their supplements will be made.—FRANK E. MORAN.

ENTOMOPHAGOUS INSECTS. By Curtis P. Clausen. McGraw-Hill Book Co., New York, 1940. 688 pp., 257 figs. \$7.00.

Becoming acquainted with an interesting new book is always a pleasant undertaking, and is especially so when, as in this instance, such book has been written by one long an internationally known authority on the subject, and when it represents the work of a

personal friend and the completion of a particularly gruelling, long-continued task, in the progress of which one has had a friendly and sympathetic interest. The study of a work of this character tends to make more vivid a realization of the very large part that entomophagous insects play in the whole insect economy, and their truly vast importance in "the maintenance of equilibrium in the insect population at a sufficiently low level to permit the existence of plant and animal life as we know it today," for entomophagous insects, as is here pointed out and emphasized, comprise a very considerable portion of the total insect population. As would be expected, the arrangement of the subject matter of the book, following a brief general introduction, has been made by orders, and begins appropriately with Hymenoptera, comprising 7 designated superfamilies and 70 families and covering 339 pages; and continues with Diptera, 36 families, 87 pages; Coleoptera, 39 families, 57 pages; Hemiptera, 6 families, 6 pages; and very brief treatment of twelve remaining orders. Following a resume of the more distinctive attributes of each order, variations in habits and adaptations, host preferences and the like, consideration is given to such matters as placement of eggs in relation to host, egg-larval parasites, unisexual reproduction, polyembryonic reproduction, phoresy, and immature stages. The various families are then taken up one by one not only in relation to the attributes of the family as a whole, but specifically in such matters as biology and habits of adults, development of immature stages, pupation, life cycle, reproductive capacity, sex ratio and parthenogenesis, effect of parasitism upon host, and the like. There are, of necessity, interesting variations in the scope and length of these discussions due to the scarcity or abundance of recorded data concerning the particular species under consideration. Groups which possess high degrees of specialization in host relationships, notably in the ways by which immature stages adapt themselves to their mode of life, have been given particular attention. Generalized predators, however, are considered only sufficiently to show habits and host preferences of respective groups. It is no longer possible for students in any highly specialized field of research, and, more particularly field workers, to have access to more than a small part of its literature for it now assumes "formidable proportions." Nor is it feasible for them to gain familiarity with more than a portion of even the more important contributions that have appeared from year to year in various languages over the world. More honor, therefore, to those who, like the author of this book, have attempted to sift, evaluate, and prepare trustworthy digests and interpretations of, or incorporate into their own writings, such accumulated knowledge. Enormous patience and persistence is imperative in bringing such tasks to successful completion. The references cited throughout are arranged by authors in one alphabetical list at the end of the book rather than at the end of the respective chapters, and, though with characteristic modesty, the author disclaims any attempt at a complete bibliography of the subject, this list of references covers 47 pages and comprises approximately 1150 separate citations, their completeness a grateful contrast to the sloppy, highly skeletonized citations annoyingly common in too many other present day scientific works. Following this, there is a carefully prepared, easily usable 27 page index to the entire volume, in which all more important page numbers are indicated in bold face type. A number of the illustrations have been prepared by the author, and those from other sources have been reduced in scale where necessary, and have been selected with admirable care to bring out more clearly corresponding text discussions. In a work of this character, refinements of literary style are not to be expected, conversely, extremely "heavy reading" is more likely to be encountered; therefore, mention should be made of the pleasing clearness of sentence structure throughout and the lucidity and sheer readability of the component parts making up this book. Ease in reading is one of the products and is eloquent of the toil and pains expended in its composition.

On the whole, the scope and contents of this book appear to be excellently epitomized in the statement by its author in its preface that "The present volume represents, as nearly as possible, what the author himself would like to have had available while engaged in field work upon insect parasitology and the biological control of insect pests." It may be added truthfully that this objective has been realized to a degree that surely will reward the author's labors with the lasting gratitude and the admiration of all those workers for whom the book has been prepared.—J. S. WADE.

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